Fishery Bulletin

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Seattle, Washington

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Fishery Bulletin

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SIZE, AGE, SEXUAL MATURITY, AND SEX RATIO IN OCEAN QUAHOGS, *ARCTICA ISLANDICA* LINNÉ, OFF LONG ISLAND, NEW YORK

JOHN W. ROPES, STEVEN A. MURAWSKI, AND FREDRIC M. SERCHUK[1]

ABSTRACT

Ocean quahogs, *Arctica islandica*, were collected off Long Island, New York, in 1978 for a determination of sexuality and gonadal condition. A microscopic examination of histologically prepared tissues of 133 clams, 19-60 mm in shell length, revealed that 36 were in an undifferentiated condition and could not be sexed. Sexual differentiation was evident in 97 clams; of the latter, 69 were in two types of intermediate development: those with sparse (20) and moderate (49) tubule development. Only 28 clams were fully mature. Age and growth were assessed from acetate peels of shell cross sections. Determinations of sex of these, and of specimens 57-103 mm in shell length collected from the same area in 1980, indicated that the smallest and youngest ocean quahogs were predominantly male, but the largest and oldest were predominantly female.

Ocean quahogs, *Arctica islandica*, like most other bivalves, lack external characteristics for a determination of sex, maturation, and gonadal condition. Sex determination has been made for other bivalves, such as the surf clam, *Spisula solidissima* (Ropes 1979a), from microscopic examinations of gametogenesis in histological preparations of gonadal tissues. Similar examinations were lacking for ocean quahogs. The resource has become an important fishery within the past half-decade (Ropes 1979b; Serchuk and Murawski 1980[2]).

In most bivalves that have been studied, sexual maturity occurs at a young age and small size, but species differences have been observed (Altman and Dittmer 1972). Thompson et al. (1980a, b) found that the ocean quahog is a slow growing, long-lived species which exhibits considerable variability in maturation with respect to size and age. The latter conclusion was based on examinations of 39 specimens, 87% of which were 40 mm or longer in shell length. The samples were collected in April-May, 3-4 mo before the spawning period reported for this species by Loosanoff (1953). It seemed reasonable to assume that mature, older quahogs in the sample would produce large numbers of sex cells, but it was not possible to determine whether most of the undifferentiated gonads in the sample would do likewise. Their contribution to the reproductive potential of the species was an enigma, and our knowledge of maturation was incomplete.

In late July and early August 1978, the National Marine Fisheries Service marked large numbers of ocean quahogs at a location near a site sampled in the study of sexual maturity reported by Thompson et al. (1980b). This was an opportunity to collect specimens for a reexamination of gonadal condition at about the time of maximum ripeness, as Loosanoff (1953) had reported finding many ocean quahogs in the partial spawning condition in mid-August. The time of collection, then, seemed favorable for obtaining sexually mature quahogs with fully developed, ripe gonads that could be clearly separated from immature quahogs with undifferentiated sex cells in the gonads.

METHODS

A commercial clam dredge vessel, MV *Diane Maria*, was chartered for the marking project during 25 July-5 August 1978. The hydraulic clam dredge had a 100-in (2.54 m)-wide knife and was modified by lining the inner surfaces with 1/2-in (12.7 mm) square-mesh hardware cloth to retain small clams. Sample tows were of 4-5 min duration and usually resulted in a dredge filled with clams, shells, and bottom substrata.

[1]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]Serchuk, F. M., and S. A. Murawski. 1980. Evaluation and status of ocean quahogs, *Arctica islandica* (Linnaeus) populations off the Middle Atlantic coast of the United States. Woods Hole Lab. Ref. Doc. 80-32, 4 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

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The sample site was 48 km SSE of Shinnecock Inlet, Long Island, N.Y., at lat. 40°21'N, long. 72°24'W, and 53 m deep. This location contained high densities and a wide size range of ocean quahogs and had a low probability of being disturbed by the fishery: criteria important for success in the marking experiment (Murawski et al. 1982). The wide size range of ocean quahogs found at and near the site included more small individuals for a study of maturity than elsewhere in the Middle Atlantic Bight.

Small quahogs (<65 mm shell length) were sorted from the catch during the marking operation, and the soft bodies were immediately removed from the shells for preservation in Bouin's fixative; shells were saved and coded for reference to corresponding tissues. Slides of the gonadal tissues were prepared for microscopic examination using standard histological techniques. The clam bodies were cut dorsoventrally through the midsection, and the anterior and posterior pieces of each clam were embedded to produce two sections for examination. The 6 μm thick sections were stained in Harris' hematoxylin and eosin. Recognition of gametogenic stages was based on previous studies of bivalve reproduction by Loosanoff (1953); Ropes and Stickney (1965); Ropes (1968a, b; 1971; 1979a); Thompson et al. (1980b); Jones (1981); and Mann (1982).

The shells were processed for observation of internal age/growth lines in acetate peels by methods similar to those reported in Thompson et al. (1980a, b) and reported more fully by Ropes (1982)[3]. A radial section was made from the umbo to ventral margin of left valves, since these contain a single prominent tooth that Thompson et al. (1980a, b) found had growth lines corresponding in number to those in the valve. Proper orientation of the valve for sectioning to retain the umbonal portion and broadest tooth surface in the anterior portion of the valve was a critical procedural step. The sections were made on a low-speed saw and by a 10.2 cm diameter by 0.03 cm thick diamond wafering blade. The cut edges were hand polished on wetable carborundum paper (240, 400, and 600 grits) to remove saw marks, polished to a high luster on a vibrating lap machine charged with aluminum oxide, then etched in a 1% HCl solution for one min. Peels were produced by flooding the etched surfaces with acetone and applying 0.127 mm thick acetate film. After a 15-min drying period, the film was peeled off and sandwiched between glass slides. Peel images were enlarged on a microprojector to 40×. Age/growth lines were counted and the exit location of each at the external edge was marked on the peel for a comparison with the external bands by placing the anterior valve portion on the peel image. This procedure clearly demonstrated correspondence between the number and location of internal lines and external bands. It also delimited sequential increments between external bands for measurement to the nearest 0.1 mm with calipers.

Periodic age/growth phenomena in the shells of ocean quahogs have been called "bands" for increments of darker periostracum deposits on the external shell surfaces and "lines" for those accreted in the shells. The latter have been identified as prismatic microstructures that demark boundaries of growth increments (Ropes et al. in press); the external pigmented bands varied in intensity and width (from 0 to ~2 mm). A slight concentric depression often outlined the shell shape in the bands and corresponded to the location of internal lines. This and the method of marking the acetate peel aided in measuring increments of growth.

After completing the study of the gonadal tissues of small ocean quahogs, it was evident that the sex ratio of larger clams from the same area should be examined. Therefore, squashes of thawed gonadal tissues from 199 marked clams 57-103 mm shell length recaptured in August 1980 were examined microscopically at the laboratory for determination of sex.

RESULTS

Observations of Age

The shells and acetate peels of 137 clams were examined. Bands on the external shell surfaces were not equally distinct for all clams in the sample. The bands were widely separated for small clams, but crowded together at the ventral margin for large clams. A few shells had poorly defined bands, but lines in the peels aided in locating them. Age annuli formed during the earliest ontogeny of ocean quahogs are difficult to detect on the valve surface and must be carefully exposed in the sectioned shell. A quahog 20.0 mm in shell length had three barely detectable bands on the surface of its valves; the two most recent annuli in peels of the valve and hinge tooth were most obvi-

[3]Ropes, J. W. 1982. Procedures for preparing acetate peels of embedded valves of *Arctica islandica* for ageing. Woods Hole Lab. Ref. Doc. 82-18, 8 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

ous and the first was confounded by a secondary incomplete line that had formed slightly later (Fig. 1a, b). The formation of secondary lines is not typical at a young age. The formation of a complete line is, however, important in detecting annuli.

Three clams had shell abnormalities related to an injury. An ocean quahog with six bands had a slight depression at the anterior end of the left valve that was not detected as unusual growth lines or increments in the peel of either the valve or tooth; the right valve showed no evidence of an injury (Fig. 2a, b). Another quahog had a deep indentation, and part of the ventral margin was missing in the left valve before band six had been formed, but the right valve showed a slight indentation and darkening as evidence of an injury (Fig. 3a, b). The peel of the left valve showed age lines before and immediately after the site of the injury (Fig. 3c). The sixth annuli in the hinge tooth was very prominent (Fig. 3d). The valve of a quahog with seven bands had definite surface indentations associated with annuli, and the hinge tooth showed regularly spaced growth increments (Fig. 4a, b, c). An injury was not clearly evident. The annuli in peels of all these clams were easily related to bands on the valve surface for measurements of growth.

For 9 clams (47.5-60.4 mm long), all annuli in the peels were counted, but only some bands were measured because those near the ventral margin were too crowded and poorly defined.

The shells of 3 clams (39.7-64.0 mm long) produced a confused pattern of lines in the ventral third of the peels and extensive ridging and poorly defined bands on the external valve surfaces (Fig. 5a, b, c). It was not evident that these clams had been injured, but they were omitted in analyses, since growth appeared to be aberrant. In all, 134 clams, 18.7-60.4 mm long and averaging 38.9 mm (S.D. ± 8.65), were used.

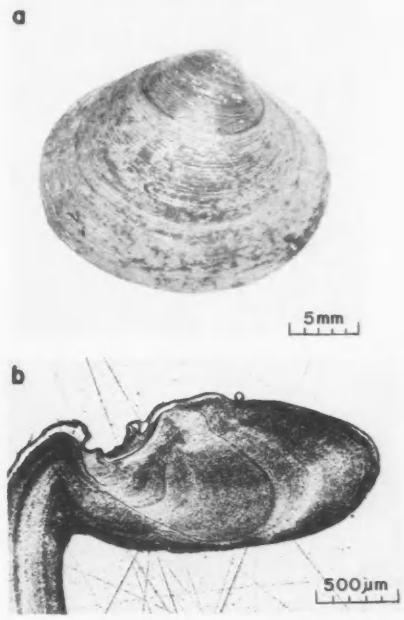


FIGURE 1.—(a) Right valve of a 3-yr-old ocean quahog, *Arctica islandica*, 20.0 mm shell length. (b) Photomicrograph of the acetate peel image of the hinge tooth showing three annuli.

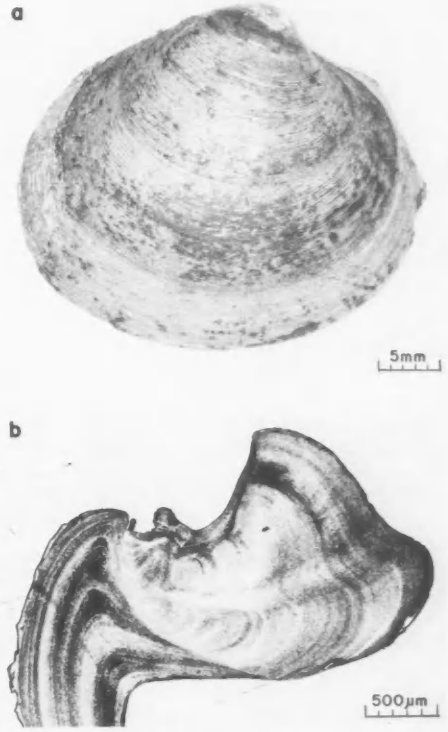


FIGURE 2.—(a) Right valve of a 6-yr-old ocean quahog, *Arctica islandica*, 31.1 mm shell length. (b) Photomicrograph of the acetate peel image of the hinge tooth showing six annuli.

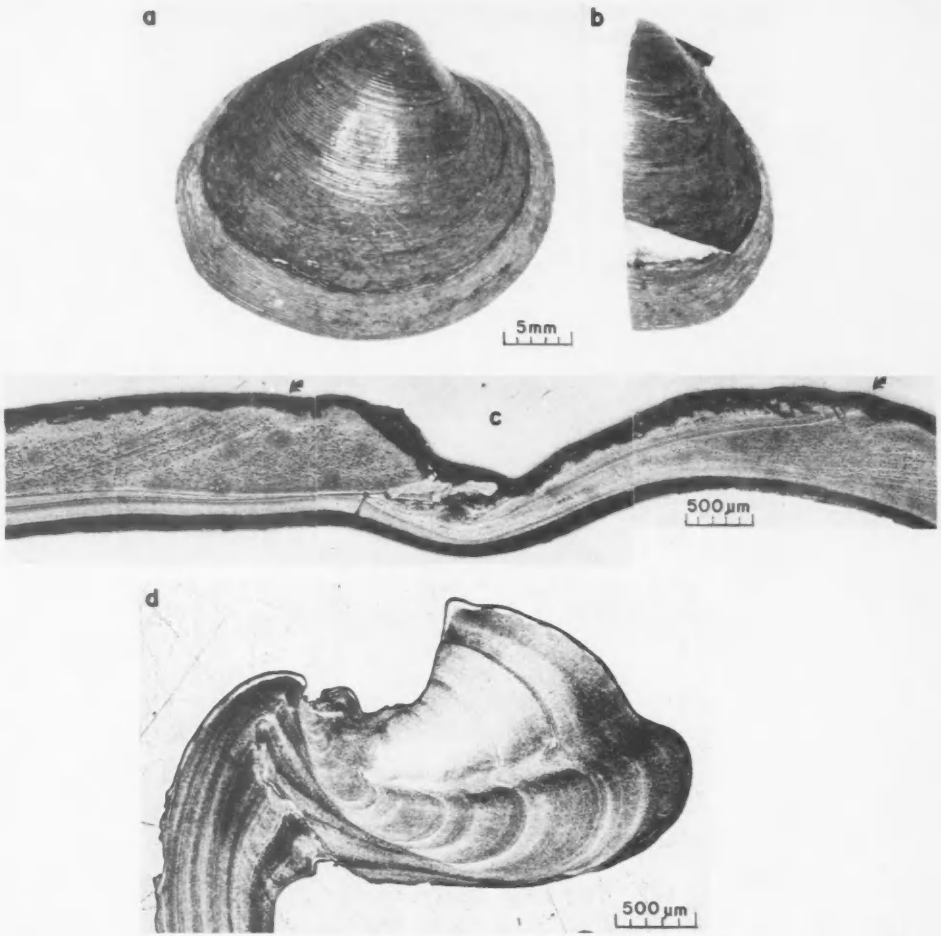


FIGURE 3.—(a) Right valve of a 6-yr-old ocean quahog, *Arctica islandica*, 33.1 mm shell length. (b) Sectioned anterior portion of the left valve showing injury. (c) Three serial photomicrographs of the acetate peel image. Arrows point to annuli formed before and after the injury. (d) Photomicrograph of the acetate peel image of the hinge tooth showing six annuli.

Size measurements at age of the clams are shown in Figure 6. The mean shell length, one standard deviation from the mean, and range are given for clams 3-8 yr old. The bands on the shells and lines in the peels indicated rapid growth through age 8. From age 3 and a mean size of 23.4 mm, the clams increased about 5 mm in shell length each year to age 8 and a mean size of 46.1 mm. Thereafter, growth seemed to decrease in rate. The bands were well separated to age 13. The bands at the ventral margin of 14-yr-old and older clams were too indistinct for accurate measurements, but the growth lines in peels were clearly separated and easily counted. The oldest 14- to 18-yr-old specimens may have been the smallest and slowest growing individuals in their year classes, but mean lengths were not progressively smaller than means for clams 9-13 yr old. Thus, a significant bias was not clearly indicated in the selection of older specimens.

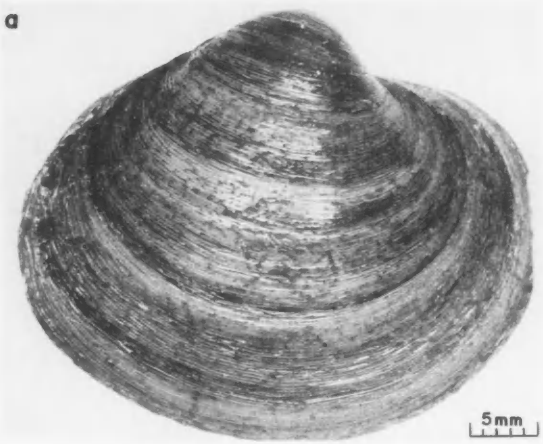
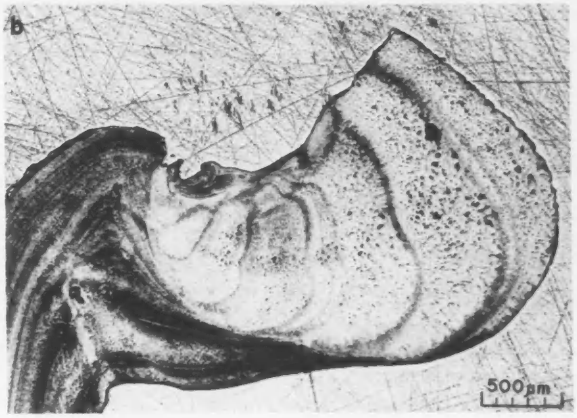
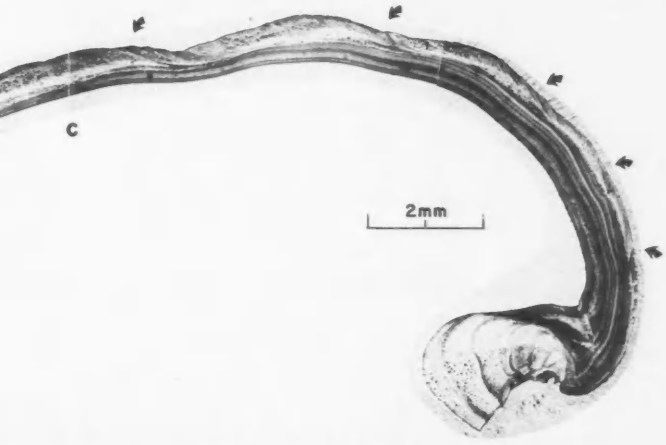
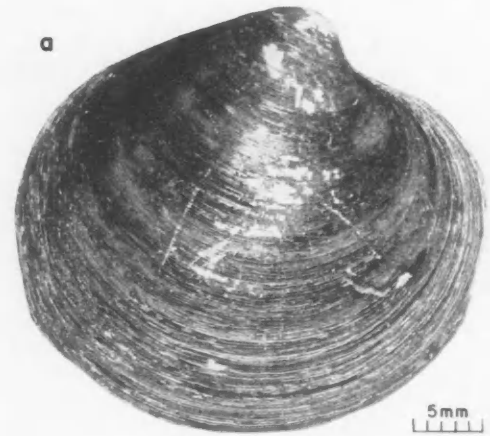


FIGURE 4.—(a) Right valve of a 7-yr-old ocean quahog, *Arctica islandica*, 35.6 mm
seven annuli. (c) Four serial photomicrographs of the se





.6 mm shell length. (b) Photomicrograph of the acetate peel image of the hinge tooth showing
f the sectioned left valve with arrows pointing to annuli in the valve.



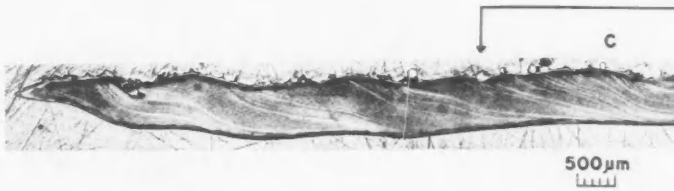


FIGURE 5.—(a) Right valve of a 40.0 mm shell length ocean quahog, *Arctica islandica*. (b) P
photomicrographs of the acetate peel image of the sectioned valve at the ventral margi

(b) Photomicrograph of the acetate peel image of the hinge tooth. (c) Three serial
margin. Brackets show a zone of poorly defined and incomplete growth lines.

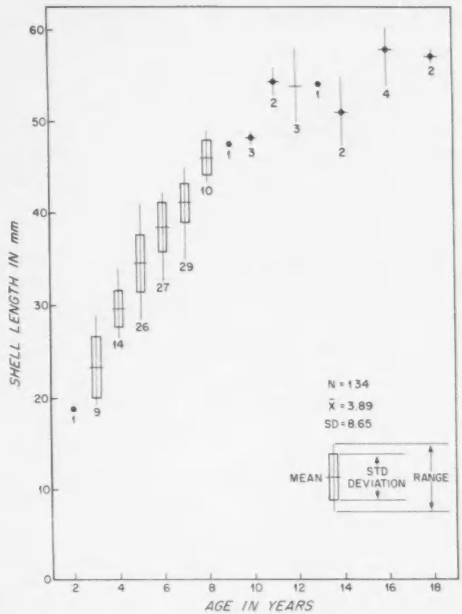


FIGURE 6.—Observed shell lengths at age of ocean quahogs, *Arctica islandica*, off Long Island, N.Y., late July-early August 1978.

Observations of Gonadal Condition

Gametogenesis

Gametogenesis in pelecypod molluscs exhibits similar basic characteristics. Each reproductive cycle begins with the production of the smallest, earliest cells at the basement membrane of follicles or alveoli. These infiltrate the lumina during maturation. Spermiogenesis through meiotic divisions is completed within male gonadal alveoli; oogenesis undergoes mitotic division of the oogonia and growth of the primary oocytes within the female gonadal alveoli. Oocytes may reach metaphase of the first meiotic division in the ducts of spawning females, but are blocked from completing maturation until after spawning and sperm penetration (Raven 1958). Most pelecypods expel the ripe cells into the surrounding environmental water where fertilization and larval development occur. A few pelecypods, and most notably female oysters of the genus *Ostrea*, are exceptions, since the eggs are held in the inhalent cavity during fertilization and initial developmental stages (Yonge 1960). A reproductive cycle corresponds to the initiation and completion of gametogenic stages and spawning. Single annual cycles have been described for many pelecypods, including the ocean quahog, although biannual and continuous cycles have been discribed for others (Sastry 1979). In some species, such as the ocean quahog, successive reproductive cycles begin at or soon after spawning; in others, activation of a cycle is delayed and the gonads are considered to be in a quiescent or resting stage (Sastry 1979). The latter condition frustrates determination of sex, since secondary sexual characteristics are generally lacking in most pelecypods.

Spermiogenesis

Spermatogonia about 5.5 μm in diameter are the initial germinal cells produced by male *Arctica islandica* during a mitotic phase of spermiogenesis. Successive meiotic stages follow and include primary and secondary spermatocytes (~3.7 and 4.0 μm in diameter, respectively), spermatids (~2.2 μm), and flagellated spermatozoa. The respective cells proliferate into the lumina of alveoli. Sperm have conical heads ~4.8 μm long.

Oogenesis

Oogonia are the initial germinal cells produced by female *Arctica islandica* during oogenesis. These are embedded in the basement membrane and are comprised of cytoplasm and a conspicuous nucleus or germinal vesicle with a basophilic nucleolus surrounded by a network of loose chromatin. The distinction between oogonia, spermatogonia, and other cells in the basement membrane is not obvious. Primary oocytes begin protruding from the basement membrane into the lumina of alveoli and retain an attachment with it during the growth stage. The large spherical, vesicular nucleus of primary oocytes is surrounded by a coarse cytoplasm containing granules of the golgi apparatus and acidophilic granules of proteid yolk (Raven 1958; Kennedy and Battle 1964). The nucleolus differentiates into an amphinucleolus with maturation. Mature oocytes appear free in the lumina of alveoli and are often of irregular shape and have a distinct vitelline membrane. Measurements of the diameter of 50 clearly spherical oocytes that were sectioned through the nucleus and amphinucleolus ranged from 49.4 to 65.0 μm and averaged 56.6 μm.

Thirty-six gonadal tissues were in an undif-

ferentiated condition (Table 1, Fig. 7a, b). Gonadal tubules were of small diamater, few in number, and surrounded by an abundant loose vesicular connective tissue. Gonia embedded in the germinal epithelium lacked definite cellular structures for sex determinations. The lumina of tubules were empty.

Sex determinations were possible for 97 quahogs, but in most (69) the gonads appeared to be in an intermediate stage and not fully developed. These latter tissues were separated into two categories: Those with either sparse or moderate tubule development.

Differentiated gonads with sparse tubule development were characterized by a limited number of gametogenic cells, as well as a limited number of tubules. The 16 male tissues examined were producing a few sperm; the 4 female tissues examined were producing a few oocytes. Abundant loose vesicular connective tissue occurred between the widely spaced gonadal tubules. In males, spermatogenic cells at the germinal epithelium were about one layer thick, but were absent in portions of the epithelium (Fig. 8a, b). Some sperm were in close contact with the spermatogenic cells and a few were scattered in the lumina of tubules. In females, the few small oocytes occurred at the germinal epithelium, none were in the tubule lumina, and all were in an early developmental stage (Fig. 8c, d).

For differentiated gonads with moderate tubule development, 39 males examined were producing sperm, while 10 females examined were producing oocytes. The gonadal tubules were more numerous than in gonads of sparse tubule condition, and some exhibited an expanded alveolar condition. Loose vesicular connective tissue clearly separated the tubules. In males, several layers of spermatocytes proliferated from the germinal epithelium with some sperm forming a fringe extending toward the empty lumina; however, portions of the germinal epithelium in some tubules

TABLE 1.—Gonadal condition relative to age, sex, and size of three categories of ocean quahogs, *Arctica islandica*—sexually immature, intermediate, and mature—off Long Island, N.Y., late July-early August 1978. M = male; F = female.

	No. clams (%)							
		Intermediate						
		Tubule development						
	Immature (undifferentiated)	Sparse		Moderate		Mature		Total no.
		M	F	M	F	M	F	
Age (yr)								
2	1(0.8)							1
3	4(3.0)	2(1.5)		2(1.5)				8
4	7(5.3)	5(3.7)		2(1.5)				14
5	11(8.2)	4(3.0)	1(0.8)	9(6.7)		1(0.8)		26
6	9(6.7)	3(2.2)	(1.5)	10(7.5)		2(1.5)	1(0.8)	27
7	3(2.2)	2(1.5)	1(0.8)	12(9.0)	9(6.7)	2(1.5)		29
8	1(0.8)			3(2.2)	1(0.8)	5(3.7)		10
9						1(0.8)		1
10				1(0.8)		2(1.5)		3
11						1(0.8)	1(0.8)	2
12						1(0.8)	2(1.5)	3
13						1(0.8)		1
14						1(0.8)	1(0.8)	2
15								
16							4(3.0)	4
17								
18						2(1.5)		2
Age range	2-8	3-7	5-7	3-10	7-8	5-18	6-16	2-18
Mean	5.03	4.63	6.00	6.08	7.10	9.79	13.22	6.71
Shell length (mm)								
<20	2	0	0	0	0	0	0	2
20-29	8	4	0	3	0	0	0	15
30-39	16	9	3	18	2	2	0	50
40-49	10	3	1	18	8	12	1	53
50-59	0	0	0	0	0	5	6	11
>59	0	0	0	0	0	0	2	2
Length range	19-46	21-44	36-42	20-48	39-45	36-58	41-60	19-60
Mean	34.4	33.8	38.4	37.2	41.8	47.1	55.0	39.0
Total no.	36(27.1)	16(12.0)	4(3.0)	39(29.3)	10(7.5)	19(14.3)	9(6.8)	[1]133

[1]The tissues of a 21.1 mm, 3-yr-old clam were too poorly prepared for examination.

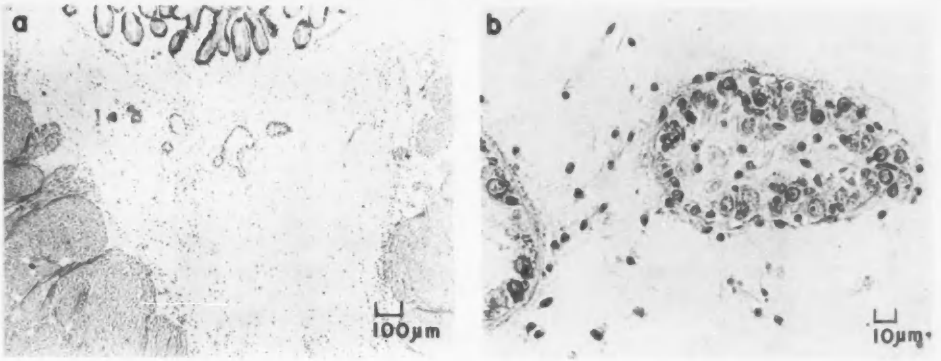


FIGURE 7.—(a) Undifferentiated gonadal tissue section from a 5-yr-old ocean quahog, *Arctica islandica*, 37.2 mm shell length. (b) Enlargement of a gonadal tubule from the same clam.

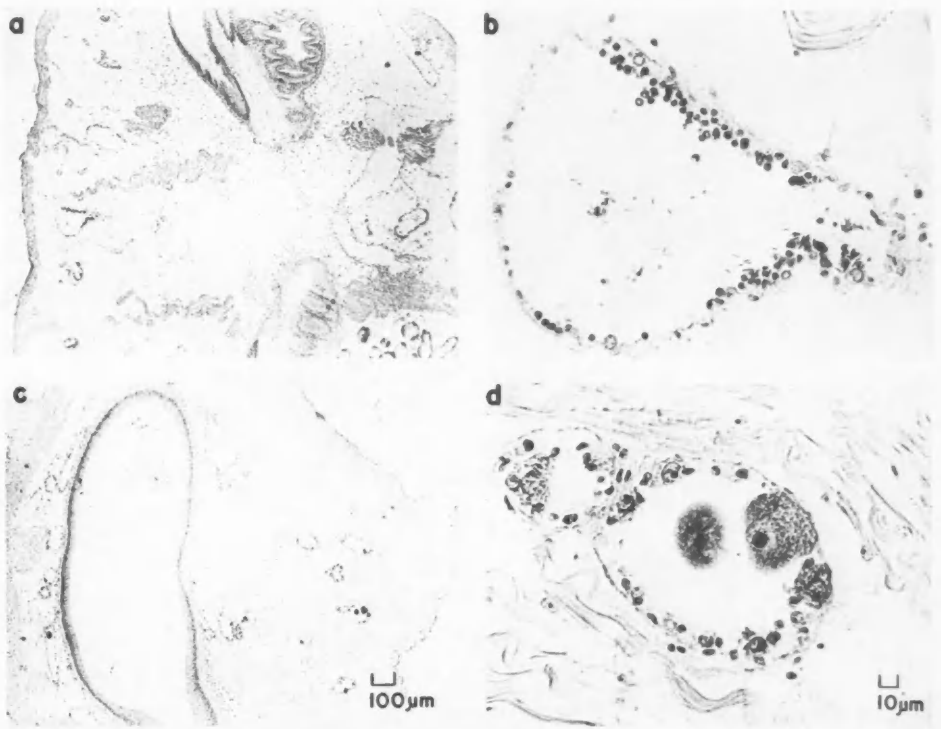


FIGURE 8.—(a) Differentiated gonadal tissue section in the sparse condition from a 3-yr-old male ocean quahog, *Arctica islandica*, 21.0 mm shell length. (b) Enlargement of spermiogenesis in a portion of a gonadal tubule. (c) Differentiated gonadal tissue section in the sparse condition from a 5-yr-old, 37.5 mm shell length, ocean quahog. (d) Enlargement of oogenesis in a gonadal tubule.

again lacked obvious spermatogenic cells (Fig. 9a, b). Oocytes in females were at the same stage of development as seen for females with sparse gonadal tubules, but more were growing from the germinal epithelium and some portions of the germinal epithelium lacked obvious oogenic cells (Fig. 9c, d).

The sexually mature condition was found in 19 males and 9 females. In these quahogs the tubules were greatly expanded and filled the gonadal area; little connective tissue occurred between adjacent tubules. Developmental stages similar to those described for other bivalves by Ropes and Stickney (1965) were recognized. Two males and one female were in an early gonadal condition. Spermiogenesis and oogenesis had cellular characteristics as in gonads of moderate tubule development, but the tubules were more numerous and crowded together. Six males were in a late gonadal condition. Primary and secondary spermatocytes and spermatids were proliferating from the germinal epithelium, filling about half of the tubules and sperm crowded into the lumina. No females were found in the late gonadal condition, but 11 males and 2 females were in an advanced late stage. In males, spermatocytes and spermatids proliferated from the germinal epithelium and sperm predominated in the lumina of the tubules (Fig. 10a, b). In females, oocytes crowded into the lumina of tubules and a few seemed to be attached to the germinal epithelium. No ripe males and only six ripe females with numerous ripe oocytes crowding into the tubules were found (Fig. 10c, d). The potential for developing large numbers of germinal cells was most evident and indicative of full sexual maturity in all of these quahogs.

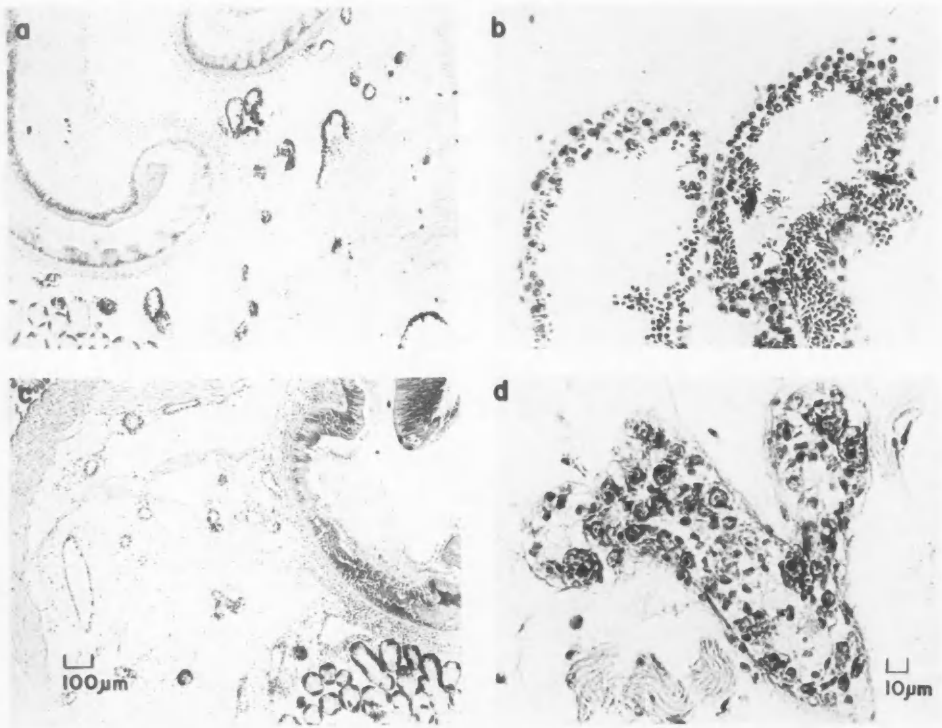


FIGURE 9.—(a) Differentiated gonadal tissue section in the moderate condition from a 7-yr-old ocean quahog, *Arctica islandica*, 42.9 mm shell length. (b) Enlargement of spermiogenesis in a portion of a gonadal tubule. (c) Differentiated gonadal tissue section in the moderate condition from an 8-yr-old female ocean quahog, 43.3 mm shell length. (d) Enlargement of oogenesis in a portion of a gonadal tubule.

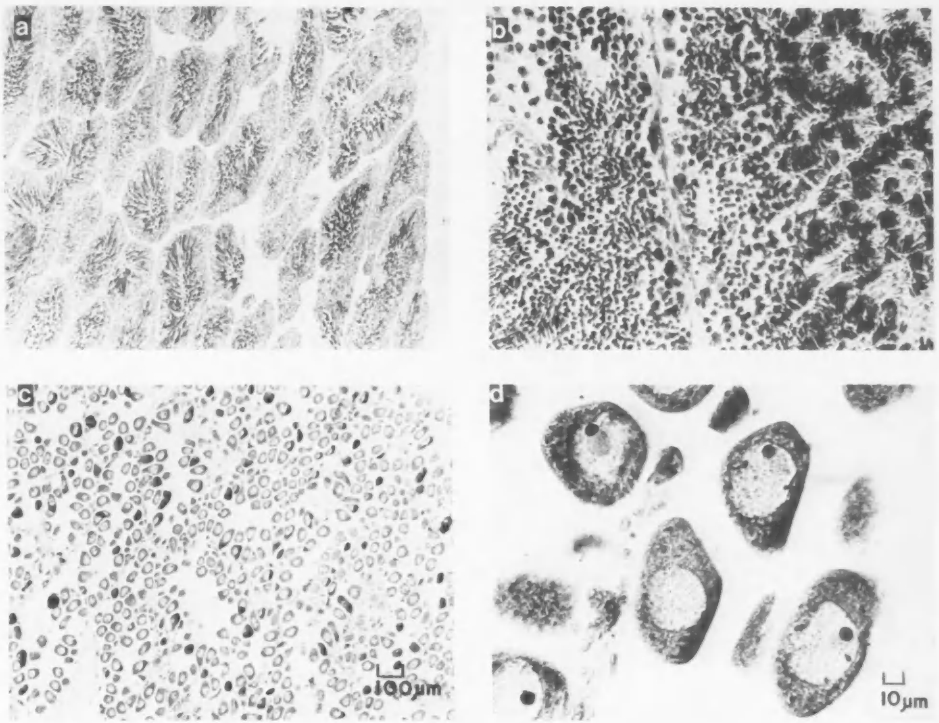


FIGURE 10.—(a) Differentiated gonadal tissue section in the mature condition from an 18-yr-old male ocean quahog, *Arctica islandica*, 57.8 mm shell length. (b) Enlargement of spermiogenesis in a portion of a gonadal tubule. (c) Differentiated gonadal tissue section in the mature condition from a 16-yr-old female quahog, 59.8 mm shell length. (d) Enlargement of ripe oocytes in a tubule.

Gonadal Condition vs. Size and Age

In an analysis of gonadal condition relative to age and size, quahogs in the undifferentiated, immature condition ranged from 2 to 8 yr old, averaged 5.0 yr old, and were from 19 to 46 mm long and averaged 34.4 mm (Table 1). This condition was found in 27% of the gonads in the sample.

For the three types of differentiated gonads, quahogs with sparse tubule development comprised 15% of the sample. Males ranged from 3 to 7 yr old, averaged 4.6 yr old, and were from 21 to 44 mm long and averaged 33.8 mm; females ranged from 5 to 7 yr old, averaged 6.0 yr, and were from 36 to 42 mm long and averaged 38.4 mm. This category contained the smallest and youngest female in the sample: 38 mm long and 5 yr old.

Quahogs with moderate tubule development comprised 37% of the sample. Males ranged from 3 to 10 yr old, averaged 6.1 yr, and were from 20 to 48 mm long and averaged 37.2 mm; females ranged from 7 to 8 yr old, averaged 7.1 yr, and were from 39 to 45 mm long and averaged 41.8 mm. This category contained the smallest and youngest male in the sample, which was 20 mm long and 3 yr old (Fig. 1a, b).

Sexually mature quahogs comprised 21% of the sample. Males ranged from 5 to 18 yr old, averaged 9.8 yr, and were from 36 to 58 mm long and averaged 47.1 mm; females ranged from 6 to 16 yr old, averaged 13.2 yr, and were from 41 to 60 mm long and averaged 55.0 mm. The smallest mature quahog found was a male 36 mm long and 6 yr old, although a 5-yr-old, 41 mm long male was also mature; the smallest and youngest mature female found was 41 mm long and 6 yr old.

None of the gonads contained germinal cells

suggestive of ambisexuality. This is consistent with the conclusion of Loosanoff (1953) that the sexes are separate. The sex ratio, however, was particularly imbalanced in favor of males. In the 69 quahogs considered less than fully mature, 55 were males and 14 were females, while in the 28 sexually mature specimens, 19 were males and 9 were females; the observed ratios were 4:1 and 2:1, respectively. The data were subjected to goodness of fit tests under the hypothesis of a 1:1 ratio between the sexes; results indicated highly significant ($P < 0.01$) and significant ($P < 0.05$) differences, respectively.

Microscopic examinations of gonadal tissue squashes of the 199 clams collected in 1980 revealed an overall sex ratio of 96 males and 103 females. These results were not significantly different from parity (1 male:1.07 female), but by separating the data into 10 mm size groups, a significant difference ($P < 0.05$) in favor of males was indicated in the size group 80-89.9 mm, and a highly signficant difference ($P < 0.01$) in favor of females was indicated in the 100-110 mm size group (Table 2).

Figure 11 shows the combined observations of clam size and sex obtained from the 1978 and 1980 samples. In these samples, males tended to decrease in occurrence relative to females with increasing shell size.

TABLE 2.—Occurrence of male and female ocean quahogs, *Arctica islandica*, within 10 mm size groups off Long Island, N.Y., August 1980.

Size group (mm)	Number	
	Males	Females
50-59	4	0
60-69	44	32
70-79	12	21
80-89	16	5
90-99	19	33
100-109	1	12
Total	96	103

DISCUSSION

The time of sampling, sample size, and capture of small quahogs provided a basis for detection of the differentiated and sexually mature stage at younger ages and smaller sizes as compared with the study of Thompson et al. (1980b). In the present study, 5- and 6-yr-old quahogs 41 and 36 mm long, respectively, were considered sexually mature; the youngest mature quahog reported by Thompson et al. (1980b) was a 42 mm male 11 yr old. The intermediate gonadal condition was found to occur at lower ages and smaller sizes than by Thompson et al. (1980b), and slightly smaller sizes were found for sexually mature quahogs. Variability in attainment of sexual maturity at age/size was observed in both studies.

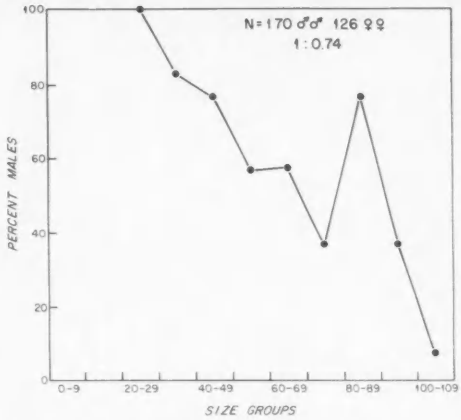


FIGURE 11.—Sex of ocean quahogs, *Arctica islandica*, relative to shell length (mm) in collections off Long Island, N.Y., 1978 and 1980.

The onset of sexual maturity at young ages has been reported for several bivalves. The bay scallop, *Argopecten irradians*, attains maturity at 1 yr; the hard clam, *Mercenaria mercenaria*, soft clam, *Mya arenaria*, and blue mussel, *Mytilus edulis*, matures at 1-2 yr (Altman and Dittmer 1972). Surf clams, *Spisula solidissima*, from an inshore habitat showed precocious sexuality in a few postlarvae or juveniles; they spawned at 1 yr, but reached full maturity at 2 yr (Ropes 1979a). Sea scallops, *Placopecten magellanicus*, spawned at about 1.5-2 yr after forming the first growth ring (Naidu 1970). In apposition to more mature gonadal conditions, some scallops in his collections were considered undifferentiated and differentiated male and female immature specimens. Lucas (1966) observed precocious sexuality in a scallop (*Chlamys varia*) and two clams (*Glycymeris glycymeris* and *Venus striatula*) from waters off France. The development of the reproductive potential during the early life history of these several bivalves seems consistent with estimates of their life span, which are as short as 2 yr for the bay scallop and as long as 30 yr for the surf clam (Belding 1906; Ropes 1979a). In contrast, the present study revealed that ocean quahogs attain maturity at 5-10 yr of age, and Thompson et al.

(1980a) reported a longevity of about 150 yr. They found that growth was vigorous at old age and that there were no obvious indications of reproductive senility. A small abyssal nuculoid bivalve, *Tindaria callistiformis*, studied by Turekian et al. (1975) seems most exceptional with regard to age and size at sexual maturity. They found a longevity of about 100 yr for a large specimen (8.4 mm shell length) by radiometric techniques and counts of shell growth bands, but gonadal development was not recognized until the clams were about 4 mm long and 50-60 yr old. The attainment of sexual maturity about midway in the life span of *Tindaria* sets it apart from other species that reproduce at a younger age. Nevertheless, all have the potential to reproduce for many years. Reproduction during a long life span of a species may be an evolutionary strategy in response to uncertain larval and juvenile survival (Krebs 1972). Reproduction during a particularly long life span is most obvious for *Arctica islandica*.

For the 69 gonads containing sexually differentiated germinal cells and sparse-to-moderate tubule development, some morphologically ripe sperm were present. In contrast, oogenesis never exceeded an early developmental state. Jones (1981), Loosanoff (1953), von Oertzen (1972), and Mann (1982) reported that mature ocean quahogs spawn each year. Thus, the sperm may be spawned, but the fate of the oocytes remains an enigma. In American oysters, *Crassostrea virginica*, germinal cells remaining in the gonads after spawning are reabsorbed (Galtsoff 1964), but viable, nearly ripe, or ripe germinal cells may be retained by hard clams throughout the fall, winter, and into the following spring (Loosanoff and Davis 1951). Thus, bivalves appear to differ greatly in this respect. No conclusion can be drawn relative to retention of germinal cells after spawning for ocean quahogs which were intermediate between the immature and mature condition in the absence of collected data.

Gonadal development in 28 mature clams suggested that many (46%) were approaching ripeness or were ripe (21%). Later development probably resulted in a spawning which was begun in late August-September. This seems reasonable based on observations by Mann (1982) of the reproductive cycle of *Arctica islandica* from sample locations in Block Island Sound. At the beginning of his study in September 1978, most (69%) were in the partially spent or spent condition and spawning was indicated until mid-November. An exact correspondence of the time and duration of spawning may be a hazardous assumption, since the two sample sites are about 110 km apart and some of the samples taken by Mann (1982) were at shallow depths (36 m).

A disparity in the initiation of gametogenesis was observed between the sexes. Male ocean quahogs began producing germinal cells at a smaller size and younger age than females. This suggests that females require a longer period of development and growth. The later development of female sexuality is a probable explanation for the highly significant difference obtained in tests of the sex ratio of quahogs in the intermediate gonadal condition. The significant difference observed for fully mature quahogs may be due to the small number in the sample (Dixon and Massey 1957), but Jones (1981) observed a similar disparity ($P = 0.008$) for quahogs > 75 mm from offshore New Jersey. In his collections 184 were males and 136 were females, a ratio of 1:0.74. Mann (1982) examined ocean quahogs that were mostly 80-100 mm long and found 185 males and 169 females, a ratio of 1:0.91. These observations suggest that spatial variation may occur in the sex ratio of ocean quahog populations, but that males are more numerous than females.

Pelseneer (1926) investigated the sex ratio of several mollusc species, including bivalves. He found more females among the older individuals of some populations and the converse among younger individuals. Coe (1936) recognized the existence of such disparities in molluscs and proposed the following hypotheses as possible explanations: 1) That males have a shorter longevity than females, because of a differential mortality rate or less resistance to unfavorable environmental conditions; 2) that the development of alternative sexual conditions is environmentally determined; and 3) that sex change may occur. Loosanoff (1953), von Oertzen (1972), Thompson et al. (1980b), and Jones (1981) all considered the species to be strictly dioecious, as did Mann (1982), although he found two hermaphrodites. These are anomalous, "accidental functional hermaphrodites" by the terminology of Coe (1943). Although Sastry (1979) hypothesized that a failure in the genetic sex-differentiating mechanism may produce some hermaphrodites, he found no evidence of a phenotypic or genetic basis for sex determination in pelecypods.

It is unlikely that ocean quahogs are protandric. This condition in a typically hermaphroditic species is characterized by the development of male organs or maturation of their products before

the appearance of corresponding female products. In *Ostrea lurida*, for example, spermatogonia are proliferated first throughout the follicles, but before the sperm mature oogonia have developed into numerous oocytes in the same follicles and the gonad has a definite intersexual character (Coe 1932). More than 90% of the young oysters exhibit the bisexual condition and no strictly male or female specimens occur. Old oysters in the female phase retain sperm balls and spermatogonia, and those in the male phase retain large and small oogonia. The two anomalous ocean quahogs found by Mann (1982) were examples of bilateral hermaphroditism, i.e., the germinal cells for each sex were in separate follicles. None of the investigators of the reproductive cycle in ocean quahogs suggested finding ambisexual conditions (Loosanoff 1953; von Oertzen 1972; Jones 1981; Mann 1982). Thus, the characteristic germinal cell development for protandry is lacking in ocean quahogs.

Sex reversal in some molluscs has been linked to castration from parasites invading the gonads, but evidence of causality was considered inconclusive by Noble and Noble (1961) and Malek and Cheng (1974). Except for the occurrence of the commensal nemertean, *Malacobdella grossa*, in ocean quahogs (Gibson 1967; Jones 1979), parasites in the species have not been reported (Ropes and Lang 1975)[4]. The causality of hermaphroditism in ocean quahogs, then, remains uncertain and evidence is unavailable that sex may be environmentally determined.

The hypothesis that female ocean quahogs may live longer than males has some support from determinations of the sex of specimens recovered from the marking site in August 1980. Based on predicted ages of ocean quahogs at the marking site reported by Murawski et al. (1982), the largest and oldest notched ocean quahogs were predominantly female. Since this may be atypical for the extensive population of ocean quahogs inhabiting the Middle Atlantic Bight, samples from other locations are being examined to determine possible spatial variations.

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FOOD HABITS AND DIETARY OVERLAP OF SOME SHELF ROCKFISHES (GENUS *SEBASTES*) FROM THE NORTHEASTERN PACIFIC OCEAN

RICHARD D. BRODEUR AND WILLIAM G. PEARCY[1]

ABSTRACT

Euphausiids were the major food of five co-occurring species of rockfishes (*Sebastes* spp.) along the west coast of North America from Vancouver Island to northern California. Copepods, decapods, cephalopods, amphipods, fishes, and other pelagic prey were also consumed but were less important to the overall diet. Two species, *S. flavidus* and *S. diploproa*, were relatively euryphagous, utilizing a high number of prey taxa. The other species, *S. pinniger*, *S. alutus*, and *S. crameri*, had a more restricted diet comprised mostly of euphausiids. The numerical composition of prey in the diet of all species was similar due to the preponderance of the two dominant euphausiid species. Diet overlaps based on weight composition were high for *S. pinniger*, *S. diploproa*, and *S. alutus* but were moderate for most comparisons involving *S. flavidus* and *S. crameri*.

The diets of *S. flavidus* and *S. pinniger* were examined in more detail to explain some of the variability associated with their food habits. Both species exhibited peak feeding periods at the same time during the day. They consumed about the same mean size of prey, although *S. flavidus* consumed a wider size range of prey. Size of prey and dietary composition did not vary much with size of fish. There were significant seasonal, geographical, and diel differences in food composition for both species, which may be a function of varying food availability.

Factors that allow coexistence of a large number of morphologically similar species have been the focus of numerous studies and continued debate in the ecological literature. Competition and resource partitioning have been reviewed in general by Schoener (1974), and for fishes by Helfman (1978). Potential competition for resources is thought to be most common in three aspects of the ecological niche in fish communities: habitat, food, and time of activity (Tyler 1972; Bray and Ebeling 1975; Ross 1977; Werner 1979; Larson 1980; McPherson 1981).

Rockfishes (*Sebastes* spp.) of the family Scorpaenidae are, a priori, interesting subjects for examining the various modes of resource partitioning. This genus is extremely speciose, with about 100 species reported from the North Pacific Ocean. At least 69 of these species are known to occur in the eastern North Pacific (Chen 1975). In addition to the large number of species, rockfishes also exhibit a high degree of overlap in their geographical distributions, with as many as 50 species occurring in a narrow latitudinal band (lat. 34°-38°N) off central California (Chen 1971). Several of these congeners are morphologically similar and occupy similar habitats, so the potential for resource overlap and competition is high (Larson 1980).

Many of these species are abundant enough and of sufficient size to contribute substantially to commercial trawl landings in the northeastern Pacific (Alverson et al. 1964; Alton 1972; Gabriel and Tyler 1980; Gunderson and Sample 1980). Despite their abundance in the northeastern Pacific, relatively few quantitative studies exist on rockfish feeding habits. Most of the studies to date have dealt with shallow-water, neritic species often taken in recreational fisheries or accessible to in situ observations and sampling by scuba divers (Gotshall et al. 1965; Larson 1972; Hobson and Chess 1976; Love and Ebeling 1978). Descriptions of the diet of offshore species of *Sebastes* generally either lack taxonomic or quantitative detail (Phillips 1964) or encompass limited geographical area or collection times (Pereyra et al. 1969; Lorz et al. 1983). Skalkin (1964) and Somerton et al. (1978)[2] described food habits of rockfishes from the Bering Sea and Gulf of Alaska, far

[1]School of Oceanography, Oregon State University, Marine Science Center, Newport, OR 97365.

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[2]Somerton, D., F. Funk, K. Mesmer, L. J. Bledsoe, and K. Thornburgh. 1978. A comparative study of the diets of Pacific ocean perch (*Sebastes alutus*) and walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. NORFISH Tech. Rep. NPB8, Wash. Sea Grant, 25 p.

north of our study area which extends from off northern California to off Vancouver Island, British Columbia.

This study represents the first attempt to examine broad geographical and seasonal patterns in food utilization and overlap by several commercially important species of rockfish on the outer continental shelf. The species considered include the yellowtail rockfish, *Sebastes flavidus*; canary rockfish, *S. pinniger*; Pacific ocean perch, *S. alutus*; splitnose rockfish, *S. diploproa*; and the darkblotched rockfish, *S. crameri*, all important members of the demersal shelf rockfish complex (Gabriel and Tyler 1980). In addition, variability in the diet of two of these species, *S. flavidus* and *S. pinniger*, was examined for the purpose of determining the effects of factors such as season, geographic area, time of capture, and predator size.

MATERIALS AND METHODS

Sampling Methods

The food utilization patterns of the five rockfish species were determined by examining stomach contents. Fishes were obtained by two different survey methods (hereafter referred to as the summer and seasonal surveys). As the collection methods differ, they will be discussed separately. The laboratory methods are similar and will be presented together.

Summer Survey Methods

Collections for the summer survey were made during the National Marine Fisheries Service (NMFS) 1980 West Coast Survey which took place from 12 July to 28 September 1980. The purpose of this survey was to assess the distribution and abundance of commercially important rockfishes. The area encompassed by the survey included much of the continental shelf and inner slope (ranging in depth from 55 to 366 m) between Monterey, Calif., (lat. 36°48′N) and the northern end of Vancouver Island, British Columbia (lat. 50°00′N). Two commercial stern trawlers, the FV *Mary Lou* and the FV *Pat San Marie*, were utilized for the survey. A Nor'Eastern[3] high-opening bottom trawl with an estimated 13.4 m horizontal and an 8.8 m vertical mouth opening was used on both vessels. The main body was constructed of 127 mm stretched mesh with 89 mm mesh in the cod end. The cod end also contained a 32 mm mesh liner. Half-hour tows were made at random depth-stratified stations chosen by a method described in Gunderson and Sample (1980).

The majority of the stomach samples used in this study were collected in August and September from north of lat. 43°N (Table 1, Fig. 1). Complete station data are given in Brodeur (1983).

Stomachs were removed at sea from a random subsample of the catch of the five target species (Table 1). *Sebastes pinniger* and *S. flavidus* were the primary target species, and stomachs of these species were collected first and the other species sampled as time allowed. Altogether, 480 stomachs were collected during the survey, all from adult fish (>200 mm FL). Fork length (measured to the nearest millimeter) and sex were recorded for all fish sampled, and stomachs were then removed, individually wrapped and labeled, and preserved in a 10% Formalin-seawater mixture. The intestinal tracts of many of the fish were examined at sea but few contained any recognizable food and none were retained. Total elapsed time between bringing the fish on board and preserving the stomachs was <1 h. The oral cavities of all fish were examined for signs of stomach eversion and regurgitation; any fish showing such signs were discarded. Individual fish weights were not recorded at sea but were later calculated using the length-weight relationships of Phillips (1964).

TABLE 1.—Number of rockfish stomachs analyzed from the 1980 National Marine Fisheries Service summer survey. The approximate latitudinal ranges covered by each leg were I, lat. 37°-42°N; II, lat. 43°-46°N; III, lat. 46°-50°N.

Leg	Sampling dates	Species	Number
I	12-20 July	*S. pinniger*	9
		S. flavidus	8
			17
II	4-29 Aug.	*S. pinniger*	85
		S. flavidus	127
		S. alutus	54
		S. diploproa	52
		S. crameri	30
			348
III	4-28 Sept.	*S. pinniger*	36
		S. flavidus	50
		S. alutus	19
		S. diploproa	10
			115
		Total number analyzed	480

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

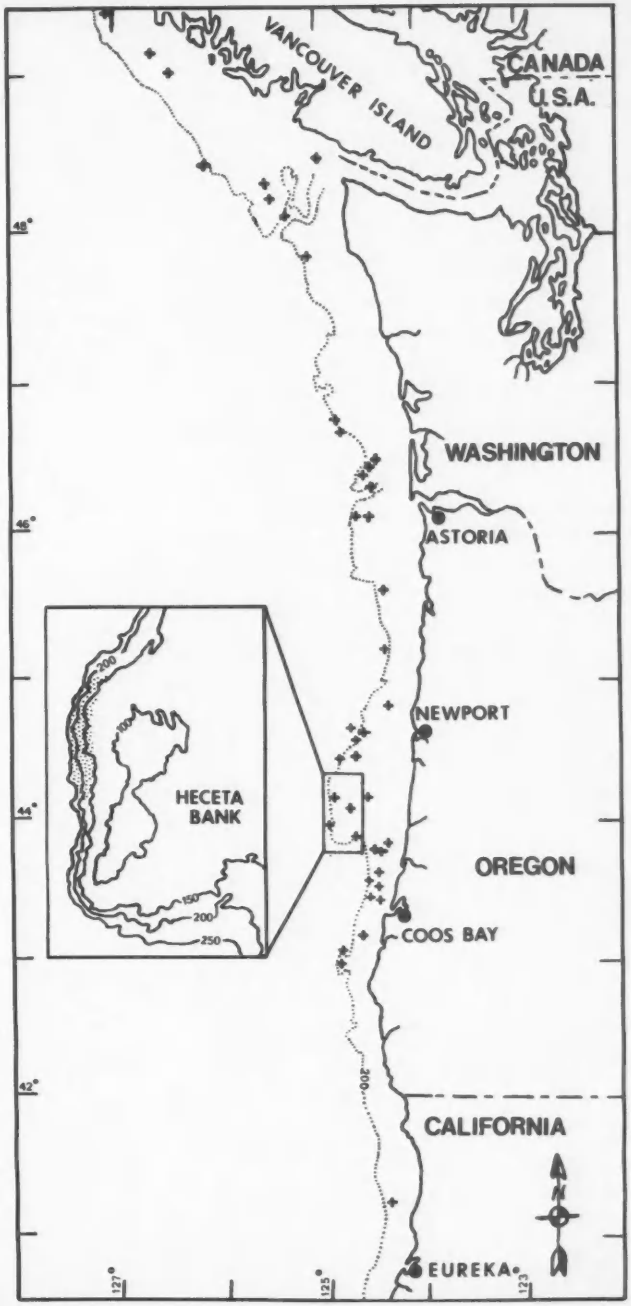

FIGURE 1.—Location of sampling stations from which stomach collections were taken. + sign denotes collections made during the National Marine Fisheries Service's summer survey and the stippled area (inset) shows the sampling area on Heceta Bank of the Oregon Department of Fish and Wildlife's seasonal collections. All depth contours are in meters.

Seasonal Survey Methods

Stomachs for the seasonal study were collected during rockfish surveys conducted by the Oregon Department of Fish and Wildlife (ODFW) on Heceta Bank off the central coast of Oregon. These surveys obtained hydroacoustic and environmental data along with the trawl catches. A total of 317 stomach samples was collected during seven surveys conducted in 1980-81 (Table 2). All surveys used trawling gear similar to that used in the summer surveys.

Locations of the tows were chosen on the basis of high concentrations of fish found during acoustic surveys over the outside edge of Heceta Bank between lat. 44°20′N and 44°00′N between the 128 m and 238 m bathymetric contours (inset, Fig. 1). The duration of tows was variable but averaged <1 h. No tows were attempted at night because of the lack of acoustical targets near the bottom at this time. Stomachs were collected as described earlier.

TABLE 2.—Number of rockfish stomachs analyzed from the seasonal Oregon Department of Fish and Wildlife collections on Heceta Bank. All dates are in 1980 unless otherwise noted.

Vessel	Cruise	Sampling dates	Species	Number
Ronnie C	I	23-24 April	*S. pinniger*	42
Bay Islander	I	17-18 June	*S. pinniger*	24
Queen Victoria	I	15-16 July	*S. pinniger*	47
			S. flavidus	16
Ronnie C	II	26-28 Sept.	*S. pinniger*	60
			S. flavidus	23
New Life	I	27 Oct.	*S. pinniger*	21
			S. flavidus	2
Ronnie C	III	17-18 Dec.	*S. pinniger*	33
			S. flavidus	25
New Life	II	25 Jan. 1981	*S. pinniger*	11
			S. flavidus	13
			Total number analyzed	317

Analysis of Stomach Contents

The stomachs were opened and their contents transferred to 50% isopropyl alcohol in the laboratory. Contents were examined using a variable power dissecting microscope. Individual stomach fullness was estimated according to a subjective rating ranging from 0 (empty) to 5 (stomach fully distended with food). The condition of the contents was assigned a value from 0 (well-digested, barely identifiable to phylum) to 4 (fresh).

Prey were identified to the lowest possible taxon and enumerated. In stomachs containing many small prey, such as euphausiids, any large or rare prey items were removed first. The remaining contents were then subdivided by means of a Folsom plankton splitter (McEwen et al. 1954), and the contents of one subsample were used to estimate the stomach contents of small prey. The digested state of the contents of many stomachs made precise counts of some prey difficult. Some paired parts of prey animals (e.g., eyes of euphausiids, otoliths of teleosts) were more resistant to digestion and total counts of these parts were halved to yield minimum counts of prey ingested. Total lengths or greatest dimensions of intact prey found in the stomach were measured to the nearest 0.1 mm for the total sample (or a subsample of at least 15 individuals) using a stage ruler or ocular micrometer. All prey were blotted dry with absorbent paper and wet weights of each taxon were recorded to the nearest milligram.

Analysis of Food Habits

The minimum number of stomach samples needed to adequately describe the diet of a species was determined for all five rockfish species, using a cumulative prey species curve. A subset of stomachs of a particular species was randomly chosen and the cumulative number of unique prey taxa were then plotted versus the number of stomachs which produced these taxa. The point on the abscissa where the curve begins to level off is considered the minimum number of stomachs necessary to describe the diet of that species. An example of the cumulative prey curves for the first 28 stomachs of each of the species in this study is shown in Figure 2. Although the curves assume different shapes, all approach an asymptote at sample sizes less than those analyzed.

The contributions of the different prey items to the total diet of the rockfishes were expressed as percent frequency of occurrence, percent numerical composition, and percent gravimetric composition. Breadth and overlap were calculated for the five rockfishes from the summer surveys and for *S. pinniger* and *S. flavidus* from the seasonal surveys, using the pooled p_i's (relative proportion of the total number or biomass of resource i used by each species) for the major taxa. These include all taxa identified to at least generic level that exceeded 0.1% of the total weight or number of all identified foods. Resource breadth was computed for each species using the following formula:

$$B = \frac{1}{\Sigma_i \, p_i^2}$$

where B equals R (the total number of prey taxa

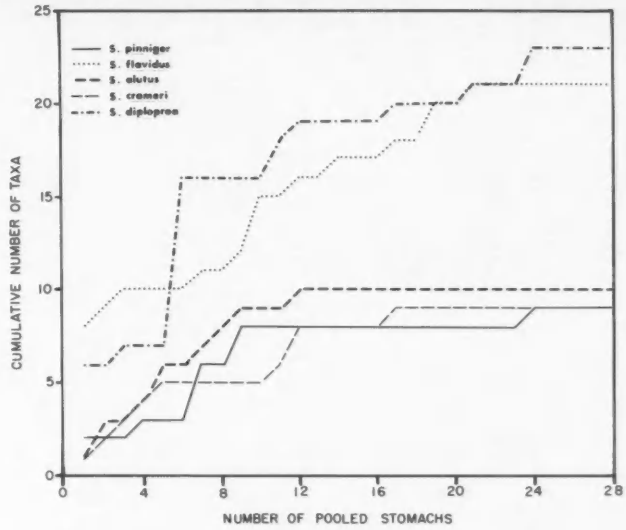

FIGURE 2.—Cumulative prey curves for the first 28 stomachs of each of the 5 rockfish species.

in a food spectrum) when all items are in equal proportion in the diet (Levins 1968). These values were normalized as $B_n = B/R$, which ranges from 0 (most uneven distribution) to 1 (totally even distribution among the prey present). This index assumes equal availabilities of the different prey to all predators.

Several indices of dietary overlap have been proposed and tested with known distributions of prey organisms (see Cailliet and Barry 1979[4]; Linton et al. 1981; Wallace 1981). The coefficient of overlap described by Colwell and Futuyma (1974; identical to Schoener's (1970) index but not expressed as a percentage) was chosen as it was found to be realistic for a wide range of true overlaps (Linton et al. 1981). This coefficient is as follows:

$$C_{ih} = 1.0 - 0.5\,(\Sigma_j |p_{ij} - p_{hj}|)$$

where p_{ij} and p_{hj} are the proportions of prey j found in the diets of species i and h respectively. This coefficient has a minimum of 0 (no overlap of prey) and a maximum of 1 (all items in equal proportions).

Analysis of Diet Variations

The sample sizes of *S. pinniger* and *S. flavidus* were sufficient to permit detailed analyses of their food habits, including seasonal, latitudinal, diel, and predator-size variations.

The 368 specimens of *S. pinniger* and 264 of *S. flavidus* were grouped into 10 mm length categories (Fig. 3). The distribution of *S. pinniger* lengths from the two surveys was similar and no significant differences in the means were found (Student's t-test; $P > 0.05$). Specimens of *S. flavidus* collected during the seasonal survey were significantly larger ($P < 0.001$) than those of the summer survey. *Sebastes pinniger* averaged about 40 mm larger than *S. flavidus* for both surveys combined. Corrections were made for this difference where appropriate in the analyses.

To simplify the analysis of dietary variation in *S. pinniger* and *S. flavidus*, eight major types of prey were selected for comparison, based on their gravimetric importance or frequency of occurrence. Numerical abundances were not used because of the great disparity in prey sizes encountered and the problem of making counts on

[4]Cailliet, G. M., and J. P. Barry. 1979. Comparison of food array overlap measures useful in fish feeding habits analysis. *In* S. J. Lipovsky and C. A. Simenstad (editors), Fish food habits studies, p. 67-79. Proc. 2d Pac. Northwest Tech. Workshop, Wash. Sea Grant.

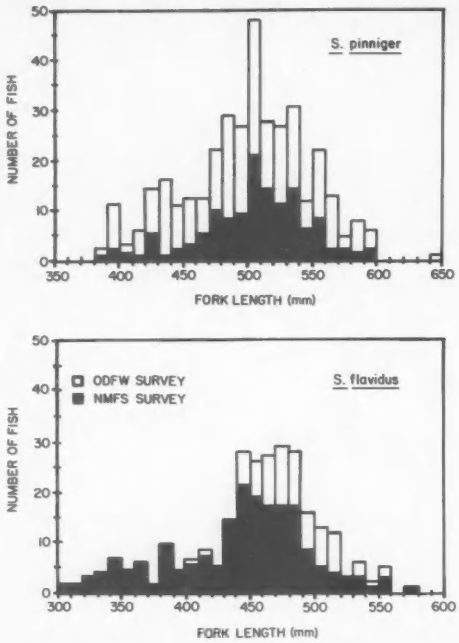

FIGURE 3.—Size distributions of *Sebastes pinniger* and *S. flavidus* from summer (National Marine Fisheries Service) and seasonal (Oregon Department of Fish and Wildlife) surveys.

incomplete animals. These prey categories include the two most important euphausiid species and other major taxonomic groups (Table 3). Other planktonic prey (e.g., copepods, chaetognaths, pteropods) were occasionally present in the diet of one or both species, but their contributions to the overall diets were minor. Cephalopods did not occur in the diet of *S. pinniger*; thus only seven prey categories were used for this species.

TABLE 3.—The major prey categories used in the analysis of diet variations and their respective size ranges found in the stomachs of *S. pinniger* and *S. flavidus*.

Category	Prey size range (mm)	Inclusive taxa or life stages
Euphausia pacifica	8-26	juvenile and adult stages
Thysanoessa spinifera	8-30	juvenile and adult stages
Total euphausiids	8-30	above two and other species, unidentified euphausiids
Decapods	3-87	adult shrimp, crab zoea and megalopae, shrimp mysis
Amphipods	3-30	mostly hyperiid but some gammarid
Cephalopods[1]	18-150+	squid and octopods
Fishes	16-150+	larvae, juvenile and adult stages
Gelatinous zooplankton	10-22	ctenophores, thaliaceans, medusae, and siphonophores

[1]Found in *S. flavidus* stomachs only.

We analyzed four factors that may affect the diet of these two species: season, geographic area, time of day, and size of fish. Each factor was subdivided into four classes to elucidate the general trends within each factor. Stomach content data for all cruises were grouped into four seasons, based on major periods in the hydrographic regime on the continental shelf off Oregon (Huyer et al. 1975; Huyer 1977): spring (March-May), summer (June-August), fall (September-November), and winter (December-February). The collection stations for all cruises were divided into one of four latitudinally defined shelf regions: Northern California-Southern Oregon (lat. 41°00′ to 43°50′N), Heceta Bank-Central Oregon (lat. 43°50′ to 45°00′N), Columbia Region (lat. 45°00′ to 47°00′N), and Northern Washington-Vancouver (lat. 47°00′ to 50°00′N).

For the analysis of diel variation of feeding, the local mean sampling time was adjusted to account for latitudinal, longitudinal, and seasonal differences in daylight. Each collection time was standardized to an equinox day with 12 h between sunrise and sunset, based on solar table values. These adjusted collection times were assigned to one of four time periods: morning (0800-1200 h), early afternoon (1200-1600 h), late afternoon (1600-1800 h), and night (1800-0700 h). Only a small number of *S. pinniger* and *S. flavidus* were collected at night despite extensive nighttime trawling effort on several occasions during the summer survey.

Since the length distributions of the two species were roughly normal (Fig. 3), dividing the length range into four equal size groups would result in disproportionately large sample sizes in the middle size ranges. On the other hand, setting the sample sizes of the four groups equal would result in narrow size ranges around the mode. As neither of these options seemed desirable, compromise groupings were chosen. For *S. pinniger*, we used the following size classes: <45 cm, 45-<50 cm, 50-<55 cm, and ≥ 55 cm. Similar size classes were selected for *S. flavidus* but were offset 5 cm to reflect the smaller mean size of this species.

To test whether significant within-factor variation occurred in the diet of each species, contingency tables were constructed comparing the occurrence of food or a particular prey category versus the absence of food or that prey category. A variance test for homogeneity of binominally distributed data (Snedecor and Cochran 1967) was

used for testing differences among the classes within each factor. Any comparisons which exceeded the tabulated 0.05 χ^2 percentage caused a rejection of the null hypothesis of similar diets.

RESULTS

General Food Habits

The results of the stomach content analysis are presented for both surveys and all five species in Tables 4 through 8. Each species will be discussed in detail in this section.

Sebastes flavidus preyed on a diverse assemblage of planktonic and micronektonic prey (Table 4). Dominating the diet in terms of frequency of occurrence (F.O.), percent by number, and, to a lesser extent, percent by weight were euphausiids, principally *Euphausia pacifica* and *Thysanoessa spinifera*. Many species of hyperiid amphipods were represented in the diet, but these were not numerous and did not comprise a major portion of the food on a weight basis. Decapods and cephalopods were moderately important in stomachs examined from both surveys. Copepods and larval decapods occurred only in the stomachs from the summer survey, while gelatinous zooplankton were found only in the seasonal study, and were common during late fall and winter. Fish were an important component on a weight basis; they were mainly mesopelagic species and juvenile stages of predominantly benthic species, although many adult Pacific herring, *Clupea harengus pallasi*, and some smelts were also found. The mean number of taxa and mean number of myctophids per stomach were higher in fish from the seasonal than those from the summer survey.

Sebastes pinniger had a much more limited diet both in number of prey species and major prey categories consumed than *S. flavidus* (Table 5). Euphausiids were again the dominant prey consumed with proportional abundances and weights exceeding 90% of the total in both surveys. Many stomachs were distended with adult euphausiids (>1,000 individuals). Hyperiid and gammarid amphipods were common but did not appear to be important components of the diet. Mesopelagic fishes, including myctophids and stomiatoids, contributed to the biomass consumed during the fall and winter months of the seasonal survey. There was a low number of taxa represented in each stomach, especially in the summer survey.

Because of the advanced stage of digestion of most of the stomach contents (mean digestion score = 1.05), many taxa were not identified to species in the stomachs of *S. alutus*, although many major prey categories were represented (Table 6). Euphausiids were the principal prey by weight and number. Of the remaining prey species, amphipods were relatively common and numerous. The oceanic shrimp, *Sergestes similis*, appeared in a significant number of stomachs and may constitute an important prey item. Remains of fishes were found in only a few stomachs, a noteworthy difference compared with the other four species examined.

Sebastes diploproa utilized a spectrum of prey items as wide as that of *S. flavidus*, but the smaller mean size of this species is reflected in generally smaller prey taken (Table 7). Euphausiids were less important, and amphipods, copepods, and decapods were more important on a numerical and percentage occurrence basis than for the other species. *Sergestes similis* contributed heavily in all respects and was found in almost half the stomachs examined. The small hyperiid amphipod, *Vibilia propinqua*, was common and numerous but contributed little to the bulk of the diet. The mean number of prey found per stomach was second only to the seasonal number of *S. flavidus*.

The diet of *S. crameri* was characterized by very few prey taxa, perhaps because only 30 stomachs were examined (Table 8). Of these, one-third of the stomachs were empty and only about one-third of the total biomass found in these stomachs was identifiable, resulting in very low mean fullness and digestion scores (1.03 and 1.05, respectively). This identifiable fraction was composed of equal numbers of euphausiids, amphipods, and copepods. Euphausiids contributed a greater share to the total biomass, however, and completely dominated the identifiable contents. Few prey taxa were found, overall, in the stomachs of *S. crameri*.

Diet Breadth and Overlap

In order to quantify the relative food resource used by the various species, niche breadth measures were calculated for all species. The principal prey types (proportional biomasses exceeding 1.0% of the total biomass), and niche breadth values (overall and normalized) are given in Table 9 for all species analyzed from the summer surveys and for *S. pinniger* and *S. flavidus* collected during the seasonal surveys.

Sebastes flavidus utilized the greatest number of prey types (R), had the widest niche breadth

TABLE 4.—Summary of yellowtail rockfish, *Sebastes flavidus*, stomach contents from the Oregon Department of Fish and Wildlife's seasonal and the National Marine Fisheries Service's summer samplings. F.O. = frequency of occurrence.

	Seasonal					Summer				
		Number		Weight (g)			Number		Weight (g)	
Prey organism	F.O. (%)	Mean	%	Mean	%	F.O. (%)	Mean	%	Mean	%
Euphausiacea										
Euphausia pacifica (juv.)	36.7	24.5	6.4	0.34	2.3	—	—	—	—	—
Euphausia pacifica (adults)	60.8	120.1	52.2	2.57	28.3	40.5	37.4	51.3	1.90	26.4
Thysanoessa spinifera (juv.)	—	—	—	—	—	6.0	11.5	2.3	0.43	0.9
T. spinifera (adults)	68.3	40.6	19.8	1.32	16.7	23.2	8.8	6.8	0.80	6.4
T. longipes	—	—	—	—	—	0.5	1.0	—	0.01	—
Thysanopoda acutifrons	1.3	1.0	—	0.12	—	—	—	—	—	—
Euphausiid unidentified	49.4	56.3	19.9	1.08	9.9	16.7	61.1	34.7	2.60	14.9
Amphipoda										
Phronima sedentaria	7.6	1.2	—	0.11	0.2	3.2	1.8	0.2	0.06	—
Paraphronima gracilis	1.3	1.0	—	0.01	—	1.1	1.0	—	0.01	—
Parathemisto pacifica	1.3	1.0	—	0.01	—	2.7	1.0	0.1	0.01	—
Hyperia medusarum	2.5	1.0	—	0.01	—	2.7	1.2	0.1	0.01	—
Hyperoche medusarum	2.5	4.0	—	0.02	—	4.9	1.7	0.3	0.89	1.5
Streetsia challengeri	3.8	1.3	—	0.03	—	0.5	1.0	—	0.04	—
Vibilia propinqua	1.3	2.0	—	0.16	—	0.5	1.0	—	0.01	—
Primno macropa	3.8	1.0	—	0.02	—	0.5	2.0	—	0.02	—
Hyperiidea unidentified	1.3	2.0	—	0.02	—	—	—	—	—	—
Rhacotropis sp.	1.3	1.0	—	0.01	—	—	—	—	—	—
Decapoda										
Sergestes similis	7.6	2.5	0.1	0.71	1.0	2.7	2.8	0.2	0.75	0.7
Pandalus jordani	1.3	12.0	0.1	3.70	0.9	1.1	1.0	—	5.19	1.9
Munida quadrispina (juv.)	3.8	9.3	0.2	0.22	0.2	2.7	5.6	0.5	0.12	0.1
Pinnotheridae megalopae	—	—	—	—	—	0.5	1.0	—	0.10	—
Cancer sp. megalopae	—	—	—	—	—	4.3	1.9	0.3	0.02	—
Decapod mysis larvae	—	—	—	—	—	1.6	2.7	0.1	0.04	—
Copepoda										
Calanus pacificus	—	—	—	—	—	0.5	1.0	—	0.01	—
C. marshallae	—	—	—	—	—	1.6	5.7	0.3	0.01	—
Neocalanus sp.	—	—	—	—	—	2.7	4.4	0.4	0.01	—
Euchirella sp.	—	—	—	—	—	0.5	1.0	—	0.02	—
Copepod unidentified	—	—	—	—	—	2.2	4.5	0.3	0.01	—
Cephalopoda										
Abraliopsis felis	1.3	1.0	—	0.93	0.2	—	—	—	—	—
Gonatus sp.	1.3	3.0	—	0.68	0.2	1.1	1.0	—	0.57	—
Loligo opalescens	3.8	1.0	—	21.24	14.9	2.2	1.5	0.1	2.26	1.7
Japatella heathi	—	—	—	—	—	1.6	1.0	—	0.68	0.3
Octopus sp. (juv.)	6.3	2.6	0.1	0.71	0.8	6.5	6.5	0.3	1.33	2.1
Cephalopod unidentified	11.4	1.2	0.1	1.82	3.8	2.2	2.2	0.2	2.34	1.7
Miscellaneous invertebrates										
Sagitta elegans	2.5	2.5	—	0.16	—	0.5	1.0	—	0.03	—
Limacina helicina	1.3	1.0	—	0.01	—	5.4	1.5	0.3	0.04	—
Alciopid polychaete	1.3	1.0	—	0.27	—	—	—	—	—	—
Siphonophora	2.5	5.5	0.1	0.54	0.3	—	—	—	—	—
Ctenophora	1.3	8.0	—	1.56	0.3	—	—	—	—	—
Cnidaria	1.3	1.0	—	0.27	—	—	—	—	—	—
Osteichthyes										
Clupea harengus pallasi	—	—	—	—	—	3.8	1.6	0.1	14.17	18.4
Thaleichthys pacificus	1.3	1.0	—	1.22	0.3	—	—	—	—	—
Spirinchus starksi	2.5	2.0	—	1.65	0.7	0.5	1.0	—	0.28	—
Stenobrachius leucopsarus	1.3	1.0	—	0.84	—	0.5	1.0	—	0.99	0.2
Diaphus theta	2.5	1.0	—	1.97	0.9	0.5	2.0	—	9.96	1.8
Tarletonbeania crenularis	5.1	1.7	0.1	4.94	4.6	—	—	—	—	—
Symbolophorus californiensis	1.3	1.0	—	0.07	—	—	—	—	—	—
Protomyctophum crockeri	1.3	1.0	—	0.14	—	—	—	—	—	—
Myctophidae unidentified	11.4	1.3	0.1	1.37	2.9	0.5	1.0	—	0.71	0.1
Argyropelecus aculeatus	1.3	1.0	—	2.49	0.6	—	—	—	—	—
Chauliodus macouni	1.3	1.0	—	3.81	0.8	—	—	—	—	—
Nectoliparis pelagicus	—	—	—	—	—	1.6	1.3	—	0.22	0.1
Liparididae unidentified	1.3	1.0	—	0.17	—	—	—	—	—	—
Stichaeidae unidentified (juv.)	1.3	2.0	—	0.44	0.1	1.1	1.0	—	0.26	0.1
Sebastes sp. (juv.)	2.5	1.0	—	0.37	0.2	1.1	2.0	—	1.07	0.4
Glyptocephalus zachirus	1.3	1.0	—	0.88	0.2	—	—	—	—	—
Lyopsetta exilis (juv.)	—	—	—	—	—	1.1	1.5	—	0.29	0.1
Psettichthys melanostictus (juv.)	—	—	—	—	—	0.5	1.0	—	0.06	—
Unidentified fish larvae	—	—	—	—	—	1.1	1.0	—	0.14	—
Fish remains	15.2	—	—	1.31	3.7	8.1	—	—	4.19	11.6
Unidentified animal remains	30.4	—	—	0.66	3.7	38.4	—	—	0.64	8.4

TABLE 4.—*Continued.*

Predator characteristics		
Number of stomachs examined:	79	185
Number of empty stomachs:	4	38
Mean weight per stomach:	5.192 g ± 7.004 (SD)	2.905 g ± 6.032 (SD)
Mean total length:	478.35 mm ± 29.06 (SD)	444.86 mm ± 51.43 (SD)
Mean fullness score:	2.87	1.92
Mean digestion score:	2.90	1.95
Mean no. prey taxa per fish:	2.81	1.55

TABLE 5.—Summary of canary rockfish, *Sebastes pinniger*, stomach contents from the Oregon Department of Fish and Wildlife's seasonal and the National Marine Fisheries Service's summer samplings. F.O. = frequency of occurrence.

	Seasonal					Summer				
		Number		Weight (g)			Number		Weight (g)	
Prey organism	F.O. (%)	Mean	%	Mean	%	F.O. (%)	Mean	%	Mean	%
Euphausiacea										
Euphausia pacifica (juv.)	21.0	88.1	12.1	0.65	4.8	3.8	12.5	0.4	0.09	0.1
E. pacifica (adults)	54.6	141.3	50.3	3.21	62.0	40.8	124.3	51.6	5.74	43.5
Thysanoessa spinifera	22.3	24.0	3.5	0.59	4.6	14.6	64.7	9.6	7.40	20.1
Thysanopoda sp.	0.4	3.4	—	0.03	—	—	—	—	—	—
Euphausiid unidentified	37.4	139.6	34.0	1.54	20.4	26.1	141.5	37.7	5.79	28.1
Mysidacea										
Inusitatomysis sp.	—	—	—	—	—	0.8	2.0	—	0.02	—
Amphipoda										
Parathemisto pacifica	0.8	2.0	—	0.01	—	4.6	1.2	—	0.01	—
Hyperoche medusarum	—	—	—	—	—	0.8	2.0	—	0.01	—
Phronima sedentaria	0.4	1.0	—	0.03	—	—	—	—	—	—
Streetsia challengeri	0.4	2.0	—	0.03	—	—	—	—	—	—
Hyperiidea unidentified	—	—	—	—	—	1.5	1.0	—	0.01	—
Rhacotropis sp.	0.4	4.0	—	0.05	—	1.5	6.0	0.1	0.07	—
Atylus tridens	0.4	1.0	—	0.01	—	—	—	—	—	—
Anonyx sp.	0.8	1.5	—	0.18	—	—	—	—	—	—
Lysianassidae unidentified	—	—	—	—	—	0.8	1.0	—	0.02	—
Decapoda										
Sergestes similis	2.9	1.7	—	0.09	0.1	1.5	14.0	0.2	1.89	0.6
Pandalus jordani	0.4	1.0	—	1.05	0.1	1.5	1.0	—	1.55	0.4
Crangon sp.	—	—	—	—	—	0.8	1.0	—	0.03	—
Munida quadrispina (juv.)	2.5	5.0	0.1	0.06	—	—	—	—	—	—
Chaetognatha										
Sagitta elegans	0.4	6.0	—	0.07	—	—	—	—	—	—
Osteichthyes										
Stenobrachius leucopsarus	0.8	1.5	—	0.78	0.2	0.8	1.0	—	0.59	0.1
Tarletonbeania crenularis	0.4	1.0	—	1.70	0.3	—	—	—	—	—
Myctophidae unidentified	1.3	1.3	—	1.47	0.6	—	—	—	—	—
Tactostoma macropus	0.4	1.0	—	1.73	0.2	—	—	—	—	—
Argyropelecus aculeatus	0.4	1.0	—	0.21	—	—	—	—	—	—
Ammodytes hexapterus	—	—	—	—	—	3.1	4.5	0.1	0.76	0.4
Sebastes jordani	0.8	1.0	—	19.04	5.6	—	—	—	—	—
Fish remains	8.4	—	—	0.39	1.2	10.8	—	—	3.00	6.0
Unidentified animal remains	12.2	—	—	0.03	0.1	42.3	—	—	0.09	0.7
Predator characteristics										
Number of stomachs examined:	238					130				
Number of empty stomachs:	39					18				
Mean weight per stomach:	2.828 g ± 4.440 (SD)					5.385 g ± 11.297 (SD)				
Mean total length:	491.45 mm ± 51.07 (SD)					504.07 mm ± 50.34 (SD)				
Mean fullness score:	2.02					1.68				
Mean digestion score:	1.89					1.55				
Mean no. prey taxa per fish:	1.27					1.00				

TABLE 6.—Summary of Pacific ocean perch, *Sebastes alutus*, stomach contents from the National Marine Fisheries Service's summer sampling. F.O. = frequency of occurrence.

Prey organism	F.O. (%)	Number of prey Mean	Number of prey %	Weight of prey (g) Mean	Weight of prey (g) %
Euphausiacea					
Euphausia pacifica	52.1	20.5	62.4	1.12	63.1
Thysanoessa spinifera	19.2	7.1	8.0	0.47	9.8
Euphausiid unidentified	20.6	16.9	20.3	0.55	12.2
Amphipoda					
Phrosina sedentaria	2.7	2.0	0.3	0.11	0.3
Paraphronima gracilis	1.4	1.0	—	0.02	—
Parathemisto pacifica	5.8	3.2	1.3	0.03	0.2
Vibilia propinqua	1.4	11.0	0.9	0.12	0.2
Primno macropa	2.7	1.0	0.2	0.02	—
Hyperiidea unidentified	6.8	2.4	1.0	0.01	—
Cyphocaris challengeri	2.7	1.0	0.2	0.03	0.1
Copepoda					
Neocalanus plumchrus	4.1	1.3	0.3	0.01	—
Eucheata sp.	2.7	3.0	0.4	0.01	—
Decapoda					
Sergestes similis	20.6	3.1	3.7	0.34	7.5
Pasiphaea pacifica	1.4	1.0	—	0.03	—
Decapod mysis larvae	1.4	1.0	—	0.01	—
Crustacea remains	2.7	—	—	0.19	0.6
Cephalopoda					
Loligo opalescens	1.4	1.0	—	0.53	0.8
Cephalopod unidentified	6.8	1.4	0.5	0.22	1.6
Osteichthyes remains	5.5	—	—	0.04	0.1
Predator characteristics					
Number of stomachs examined:		73			
Number of empty stomachs:		26			
Mean weight per stomach:		0.923 g ± 1.954 (SD)			
Mean total length:		365.36 mm ± 60.01 (SD)			
Mean fullness score:		1.49			
Mean digestion score:		1.05			
Mean no. prey taxa per fish:		1.68			

TABLE 7.—Summary of splitnose rockfish, *Sebastes diploproa*, stomach contents from the National Marine Fisheries Service's summer sampling. F.O. = frequency of occurrence.

Prey organism	F.O. (%)	Number of prey Mean	Number of prey %	Weight of prey (g) Mean	Weight of prey (g) %
Euphausiacea					
Euphausia pacifica	46.8	26.5	41.2	1.53	42.1
Thysanoessa spinifera	14.5	2.9	1.4	0.16	1.4
Euphausiid remains	29.0	34.9	33.7	1.79	30.6
Amphipoda					
Parathemisto pacifica	1.6	1.0	—	0.01	—
Hyperoche medusarum	3.2	1.0	—	0.01	—
Paraphronima gracilis	3.2	1.0	—	0.02	—
Streetsia challengeri	1.6	1.0	—	0.02	—
Vibilia propinqua	32.3	10.3	11.1	0.10	1.9
Primno macropa	3.2	1.0	—	0.01	—
Hyperiidea unidentified	9.7	1.5	0.4	0.02	0.1
Cyphocaris challengeri	4.8	1.7	0.3	0.02	—
Lysianassidae unidentified	1.6	1.0	—	0.03	—
Gammaridea unidentified	1.6	1.0	—	0.03	—
Isopoda unidentified	1.6	1.0	—	0.02	—
Copepoda					
Neocalanus cristatus	6.5	3.2	0.7	0.02	0.1
Eucheata elongata	4.8	3.3	0.5	0.03	0.1
Euchirella sp.	3.2	1.5	0.2	0.01	—
Candacia bipinnata	4.8	3.6	0.6	0.01	—
Metridia sp.	3.2	1.0	0.1	0.01	—
Decapoda					
Sergestes similis	46.8	4.4	6.8	0.60	16.5
Pasaphaea pacifica	1.6	1.0	—	0.59	0.6
Benthogenema burkenroadi	1.6	1.0	—	0.12	0.1
Munida quadrispina	1.6	6.0	0.3	0.12	0.1
Cancer sp. megalopae	9.7	1.3	0.4	0.02	0.1
Decapod mysis larvae	1.6	1.0	—	0.01	—
Mollusca					
Pteropoda unidentified	1.6	1.0	—	0.03	—
Gonatus sp.	1.6	1.0	—	0.07	—
Octopus sp. (juv.)	1.6	1.0	—	0.17	0.2
Osteichthyes					
Stenobrachius leucopsarus	1.6	1.0	—	0.36	0.3
Myctophidae unidentified	6.5	1.0	0.2	0.13	0.5
Tactostoma macropus	1.6	1.0	—	2.28	2.2
Liparididae unidentified	1.6	1.0	—	0.15	0.1
Fish remains	9.7	—	—	0.38	0.1
Unidentified animal remains	17.7	—	—	0.03	0.3
Predator characteristics					
Number of stomachs examined:		62			
Number of empty stomachs:		15			
Mean weight per stomach:		1.698 g ± 3.449 (SD)			
Mean total length:		264.82 mm ± 41.82 (SD)			
Mean fullness score:		2.50			
Mean digestion score:		1.25			
Mean no. prey taxa per fish:		2.48			

(B), and had the most even distribution among prey types (B_n) of all rockfish examined from the summer survey. *Sebastes diploproa* preyed on fewer taxa than *S. flavidus* but had moderately high overall and normalized food breadth values. *Sebastes pinniger*, *S. crameri*, and *S. alutus* utilized a similar number of distinct prey items and had similar breadth and evenness values with *S. alutus* having a more equitable distribution of prey than the other two.

The seasonal results for the *S. flavidus* and *S. pinniger* were more divergent and represent the extreme values found among the species. Seventeen principal prey types were important in the seasonal diet of *S. flavidus*, contributing toward a high B value. However, the dominance of a few species yielded a low evenness value for this species. *Sebastes pinniger* preyed on few taxa in fairly unequal proportions yielding fairly low niche breadth and evenness values. These low evenness values could be caused by the preponderance of euphausiids found in the guts of both species during the summer months.

The individual overlap coefficients and the mean overlap for each species are presented for both the weight and numerical abundance of prey in Table 10 for the summer surveys. As overlap indices are affected by the level of taxonomic specificity at which the prey have been identified, no unbiased means for testing the significance of these values are available. We adopted the convention that overlap values from 0.00 to 0.29 are considered low, 0.30 to 0.60 considered medium, and those above 0.60 show highly similar diets (Langton 1982).

The coefficients for numerical composition show high values for all possible combinations except those involving *S. crameri*. Very similar proportions of the major euphausiid prey groups resulted in an extremely high overlap value (0.93) between

TABLE 8.—Summary of darkblotched rockfish, *Sebastes crameri*, stomach contents from the National Marine Fisheries Service's summer sampling. F.O. = frequency of occurrence.

Prey organism	F.O. (%)	Number of prey		Weight of prey (g)	
		Mean	%	Mean	%
Euphausiacea					
Euphausia pacifica	13.3	8.0	37.2	0.42	26.2
Thysanoessa spinifera	3.3	1.0	1.2	0.06	0.9
Euphausiid remains	3.3	1.0	1.2	0.01	0.2
Amphipoda					
Parathemisto pacifica	16.7	4.4	25.6	0.01	1.0
Cyphocaris challengeri	6.7	1.0	2.3	0.01	0.3
Lysianassidae unidentified	3.3	1.0	1.2	0.04	0.8
Copepoda					
Neocalanus cristatus	3.3	1.0	1.2	0.01	0.2
Euchaeta elongata	10.0	3.0	10.5	0.01	0.5
Copepod unidentified	16.7	3.0	17.4	0.01	0.8
Decapoda					
Sergestes similis	3.3	1.0	1.2	0.07	1.1
Osteichthyes					
Ammodytes hexapterus	3.3	1.0	1.2	0.28	4.3
Unidentified animal remains	53.3	—	—	0.25	62.5
Predator characteristics					
Number of stomachs examined:		30			
Number of empty stomachs:		10			
Mean weight per stomach:		0.246 g ± 0.389 (SD)			
Mean total length:		330.36 mm ± 77.17 (SD)			
Mean fullness score:		1.03			
Mean digestion score:		1.05			
Mean no. prey taxa per fish:		1.26			

pinniger, *S. diploproa*, and *S. alutus* are all relatively high (0.58, 0.56, and 0.61, respectively).

Overlaps between *S. pinniger* and *S. flavidus* for the seasonal cruises are similar to the results of the summer surveys (C_{ih} = 0.80 by number; 0.46 by weight). A possible explanation for the lower values may be changes in availability of both predator and prey (i.e., no *S. flavidus* stomachs were collected during spring and early summer when the euphausiid populations are generally the highest). The variability associated with the different cruises was examined by calculating the overlaps between these two species for the four seasonal cruises that contained at least 10 specimens of each species. The July cruise had the highest overlap of all on a weight basis (C_{ih} = 0.88) and the September cruise had the lowest (C_{ih} = 0.32), while the December and January cruises had intermediate overlaps (C_{ih} = 0.52 and 0.46), suggesting seasonal variations in prey availability for these species.

For comparative purposes, the dietary composition of the five most important prey categories for each of the rockfish species is presented by percent number and percent weight in Figures 4 and 5. Both figures show the importance of euphausiids in all five species. The stomachs of *S. crameri* contained a more equitable distribution of numbers of the major prey groups than the other species of rockfishes, with higher proportions of amphipods and copepods. Some of this difference may be ascribed to the smaller sample size. On a weight basis, *S. flavidus* was unique in that fishes and cephalopods were of greater importance in the

TABLE 9.—Principal prey types making up >1.0% of the diet and food breadths of the five species of *Sebastes*. R is the total number of distinct prey items identified to at least genus level and that make up 0.1% ($p_i > 0.001$) of the identified fraction of the total weight. These prey were used to calculate the overall diet breadth (B) and the evenness of distribution of the prey items in the diet (B_n). The seasonal values for *S. flavidus* and *S. pinniger* are given in parentheses.

Species	Sample size	Principal prey types (p_i's > 0.01)	Pooled species values		
			R	B	B_n
S. flavidus	185 (79)	*Euphausia pacifica*, *Thysanoessa spinifera*, hyperiid amphipods, *Sergestes similis*, *Loligo opalescens*, myctophids, *Clupea harengus pallasi*	12 (17)	3.64 (3.77)	0.303 (0.222)
S. diploproa	62	*E. pacifica*, *T. spinifera*, *S. similis*, *Vibilia propinqua*	8	2.28	0.285
S. pinniger	130 (238)	*E. pacifica*, *T. spinifera*, *Sebastes jordani*	8 (6)	1.86 (1.33)	0.232 (0.222)
S. crameri	30	*E. pacifica*, calanoid copepods, hyperiid amphipods, *Ammodytes hexapterus*	8	1.80	0.225
S. alutus	73	*E. pacifica*, *T. spinifera*, *S. similis*	7	1.73	0.247

S. pinniger and *S. flavidus*, although the diets are not similar for other prey items.

Overlap on the basis of weight, which may be a better measure of the energy obtained from the various food items, indicates high overlap between *S. pinniger* and *S. diploproa* and between *S. alutus* and *S. pinniger*, *S. diploproa*, and *S. crameri*. The rest of the values were <0.60, including *S. pinniger* with *S. flavidus* (C_{ih} = 0.48). The diet of *S. flavidus* overlaps the least with the other species ($\overline{C}_{ih}$ = 0.42) mainly due to its more piscivorous habits. The mean overlap values of *S.*

TABLE 10.—Overlap matrix for the five species of *Sebastes*. Only those prey that have proportional abundances exceeding 0.1% were used in the analysis. Values above the rules are for proportional weight overlap and values below are for proportional abundance. The mean overlap for each species by weight and number is given in parentheses directly above and below the rules.

	S. pinniger	*S. flavidus*	*S. diploproa*	*S. crameri*	*S. alutus*	
S. pinniger	(0.58) (0.71)	0.48	0.72	0.47	0.66	
S. flavidus	0.93	(0.42) (0.70)	0.44	0.30	0.46	WEIGHT
S. diploproa	0.76	0.78	(0.56) (0.65)	0.48	0.63	
S. crameri	0.40	0.40	0.42	(0.48) (0.41)	0.69	
S. alutus	0.74	0.70	0.63	0.42	(0.61) (0.62)	
			NUMBER			

diet of this species than any of the other rockfish. Decapods were of moderate importance to *S. diploproa* and, to a lesser extent, *S. alutus*. Fishes were an important food source by weight for all rockfishes but *S. alutus*.

Seasonal Variation

Differences in the diet of *S. pinniger* and *S. flavidus* are summarized in Table 11 for the four seasons. The spring cruise shows an extreme dominance of one prey item, *Euphausia pacifica*, in the diet of *S. pinniger*. This prey species was found in about three-quarters of the stomachs and made up almost all the prey biomass. Decapod shrimp and fishes were rarely found in the diet at this time. Euphausiids also dominated the diet in the sum-

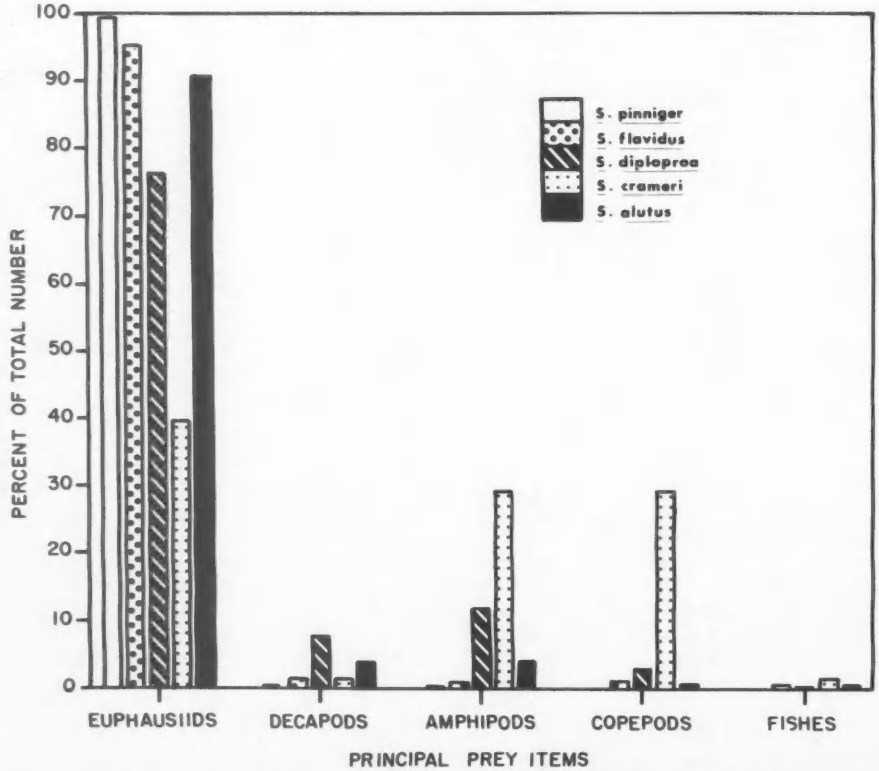

FIGURE 4.—The proportions of the five major prey taxa found in the five rockfish species based on numerical composition.

TABLE 11.—Variation in major prey taxa composition with season for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % *W* = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Species and season	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
Spring[1] (Mar.-May)	42 (14.3)	73.8	99.6	—	—	73.8	99.6	2.4	+	—	—	—	—	2.4	0.4	—	—
Summer (June-Aug.)	165 (10.9)	61.2	75.1	7.9	0.5	68.5	94.7	3.6	1.1	2.4	+	—	—	6.7	4.2	3.6	+
Fall (Sept.-Nov.)	117 (20.5)	35.9	13.8	32.5	37.8	55.6	84.2	9.4	0.2	12.0	0.1	—	—	17.9	15.1	22.2	0.3
Winter (Dec.-Feb.)	44 (22.7)	50.0	25.9	47.7	12.0	81.8	94.2	—	—	6.8	0.4	—	—	13.6	5.5	4.5	+
Sebastes flavidus																	
Spring[2] (Mar.-May)	0																
Summer (June-Aug.)	151 (16.6)	52.3	37.2	23.2	0.5	58.3	66.7	9.9	0.8	13.2	0.1	15.2	6.5	13.9	25.6	3.3	0.4
Fall (Sept.-Nov.)	75 (22.7)	34.7	6.1	42.7	29.6	54.7	42.2	9.3	13.8	26.7	0.8	6.7	1.8	28.0	40.5	10.7	0.8
Winter (Dec.-Feb.)	38 (0.0)	81.6	19.5	92.1	15.3	94.7	46.7	0.5	0.7	10.5	+	28.9	30.6	52.6	15.4	21.1	6.6

[1] All collections taken during one cruise. All other seasons represent the means of at least two cruises spaced a minimum of 1 mo apart (Tables 1 and 3 give the exact dates and samples collected on each cruise).
[2] No stomachs of *S. flavidus* were collected during this season.

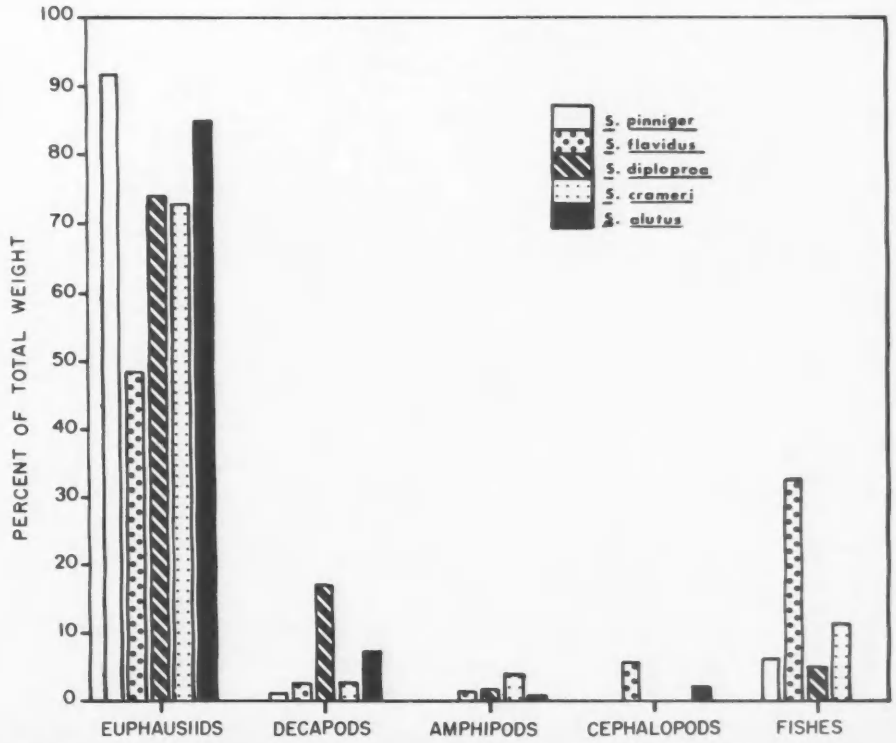

FIGURE 5.—The proportions of the five major prey taxa found in the five rockfish species based on gravimetric composition.

mer but to a lesser degree. *Thysanoessa spinifera* appeared in the stomachs at this time, but *E. pacifica* continued to be the most important euphausiid consumed. Shrimp and fishes were slightly more important but together made up only a minor portion of the diet. A low percentage of empty stomachs occurred in the summer.

The diet of *S. pinniger* in the fall showed substantial shifts in prey composition. Although the frequencies of occurrence were about equal for the two species of euphausiids, *T. spinifera* greatly exceeded *E. pacifica* by weight. Decapods were common but were represented mainly by small shrimp (*Sergestes similis*) and juvenile pelagic crabs (*Munida quadrispina*), which contributed little on a weight basis. Amphipods and gelatinous zooplankton occurred frequently but were not important by weight. Fishes were important by occurrence and weight and consisted mostly of mesopelagic species and several adult *Sebastes jordani* which made a large contribution to the biomass consumed.

Almost one-quarter of the fish collected in the winter had empty stomachs and contained much digested material. *Euphausia pacifica* and *T. spinifera* occurred in about the same number of stomachs, but *E. pacifica* contributed over twice as much of the total weight as *T. spinifera*. Subadult *E. pacifica* were very numerous at this time. The fishes consumed were mostly mesopelagic species.

Sebastes flavidus showed similar trends in food resource utilization among the three seasons from which collections were made (Table 11). Euphausiids, consisting mostly of *E. pacifica*, made up two-thirds of the diet by weight in the summer. Fishes were common and contributed heavily to the total biomass. Cephalopods were next in importance by either occurrence or weight. The diet in the fall showed the same shift in euphausiid species as was apparent for *S. pinniger*, with *T. spinifera* the dominant species. Fishes were almost as important by weight as euphausiids, but their weight total was mostly composed of adult clupeids. Cephalopods were least important in the fall months.

Euphausiids represented about half the diet during the winter, but the remainder was shared mostly by cephalopods and fishes. Both species of euphausiids were commonly found, but *E. pacifica* (mostly subadults) were slightly more important in the overall diet. Cephalopods (mostly adult *Loligo opalescens* and juvenile copepods) did show a substantial increase in weight and occurrence during these months. Fishes were found in over half the stomachs but were mainly juveniles of relatively small myctophids. Gelatinous zooplankton were most common, and decapods were least common, during this season. In contrast to *S. pinniger*, all stomachs of this species contained some food and many stomachs were full during this season.

Geographic Variation

Several trends were evident when comparing the diet of *S. pinniger* between regions (Table 12). The two southernmost regions had similar diets dominated by *E. pacifica* with *T. spinifera* representing only a minor portion of the diet. Meso-

TABLE 12.—Variation in major prey taxa composition with geographic area for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % *W* = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Area taken	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
Southern Oregon	51 (13.7)	52.9	63.1	9.8	0.6	54.9	93.1	5.8	0.8	7.8	+	—	—	5.8	6.2	5.8	+
Heceta-Central	281 (16.0)	56.9	67.1	19.6	4.4	61.2	91.3	5.3	0.8	3.2	0.1	—	—	11.7	7.6	6.4	0.1
Columbia Region[1]	0																
Washington-Vancouver	36 (16.7)	22.2	4.6	27.8	57.7	36.1	92.8	2.8	+	22.2	0.1	—	—	25.0	6.7	36.1	0.4
Sebastes flavidus																	
Southern Oregon	70 (17.1)	58.6	47.6	30.0	9.2	65.7	84.9	10.0	+	14.3	0.8	24.3	13.7	8.6	0.6	5.7	0.1
Heceta-Central	122 (11.5)	61.5	27.9	49.2	14.1	70.5	50.6	11.4	2.2	18.0	0.3	16.4	16.9	32.8	27.6	13.1	2.3
Columbia Region	22 (13.6)	27.3	3.2	9.1	0.6	36.4	12.1	18.2	1.0	4.6	+	9.1	0.3	45.5	86.5	—	—
Washington-Vancouver	50 (26.0)	28.0	7.3	34.0	12.0	48.0	20.7	12.0	17.2	16.0	0.6	2.0	1.0	26.0	60.5	4.0	+

[1]No stomachs of *S. pinniger* were collected from this region.

pelagic fishes and sergestid shrimps were common but generally contributed little to the diet on a weight basis.

The northernmost region showed reduced occurrences of euphausiids, overall, but they still composed a percent weight equivalent to the two southern areas. This could have resulted from a shift to *T. spinifera*, which is generally larger than *E. pacifica*, as the main euphausiid consumed. Decapods were of lesser importance, but gelatinous zooplankton were very common in the stomachs of fish from this region. This may explain the high abundances of hyperiid amphipods known to be associated with gelatinous zooplankton. Fishes were common, especially juvenile Pacific sand lance, *Ammodytes hexapterus*, a prey species found only in the stomachs collected from this area.

Sebastes flavidus showed a different pattern in food utilization. A general decrease in euphausiid abundance was observed with increasing latitude (Table 12). The euphausiids from the southernmost regions were mostly *E. pacifica*, although many were unidentified. The only other important prey groups in these southern regions were cephalopods (mostly *Loligo opalescens*) and relatively large fishes such as Pacific herring and myctophids (*Diaphus theta*). All other prey groups were common but made little contribution to the diet.

Specimens of *S. flavidus* collected in the northernmost regions consumed substantial amounts of fish (mainly clupeids and myctophids). Euphausiids were relatively unimportant in these regions. As was the case with *S. pinniger*, *T. spinifera* was the dominant euphausiid eaten in the Washington-Vancouver region. Decapods, consisting mostly of *Pandalus jordani*, reached their highest proportion of the diet in the northernmost region.

Diel Variation

Both species showed variation in prey composition with the diel period (Table 13). *Sebastes pinniger* contained high percentages of euphausiids by weight during all four diel periods, with highest percentages occurring in the afternoon periods. Fishes, mostly non-mesopelagic species, were most important on a weight basis during morning and night when they occurred least frequently. Euphausiids were relatively more important by weight in the two afternoon periods. A high proportion of the fishes found in the stomachs during the afternoon periods were mesopelagic species.

Sebastes flavidus exhibited the opposite trends in food consumption with respect to time of day. Euphausiids were found in the highest proportions by weight during the morning and night periods while proportions of fish were substan-

TABLE 13.—Variation in major prey taxa composition with time of day for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % W = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Time of day (h)	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
Morning (0800-1200)	68 (19.1)	25.0	32.1	19.1	5.7	51.5	83.1	7.3	0.2	13.2	0.1	—	—	8.8	15.9	23.5	0.6
Early aft. (1200-1600)	128 (10.2)	62.5	51.2	21.1	20.5	69.5	95.9	4.7	0.5	6.2	+	—	—	14.1	3.4	7.8	+
Late aft. (1600-1800)	79 (17.7)	50.6	80.2	1.6	1.8	70.9	96.3	3.8	0.7	—	—	—	—	13.9	2.9	5.1	+
Night (1800-0700)	93 (18.3)	52.7	56.8	20.4	5.9	69.9	83.4	4.3	1.4	4.3	0.2	—	—	9.7	14.8	7.5	0.1
Sebastes flavidus																	
Morning (0800-1200)	81 (18.5)	43.2	38.1	35.8	9.1	58.0	76.7	2.5	0.1	3.7	+	6.2	5.3	12.4	17.1	4.9	0.9
Early aft. (1200-1600)	71 (14.5)	54.9	25.5	28.2	7.5	57.7	48.8	14.1	4.4	19.7	0.2	15.5	7.6	25.3	37.4	7.0	1.3
Late aft. (1600-1800)	57 (17.7)	50.9	16.4	43.9	18.5	63.2	46.2	7.0	0.1	22.6	0.3	21.0	6.6	33.3	46.3	7.0	0.3
Night (1800-0700)	55 (12.7)	60.0	31.8	43.6	11.8	69.1	50.6	18.2	4.8	16.4	0.2	21.8	24.9	27.3	15.8	16.4	3.4

tially lower during these periods. Collections taken around late afternoon had equal amounts of fishes and euphausiids, while those taken at night had high occurrences and biomass of cephalopods (mostly *Loligo opalescens*) and gelatinous zooplankton.

The mean fullness score, mean digestion score, mean weight ratio (equal to the weight of stomach contents divided by weight of fish), and the percentage of empty stomachs were plotted for each adjusted collection time for both species. *Sebastes pinniger* had a distinct periodicity in its feeding cycle (Fig. 6). Peak periods of feeding intensity occurred midday and shortly after dusk. One collection (eight stomachs) taken at 0400 h had low values for fullness score and weight ratio but average values for digestion score and percentage of empty stomachs. The fullness and digestion scores (Fig. 6A) follow each other fairly well except that the midday digestion peak was several hours later than the fullness peak. A very distinct peak in the weight ratio at 1200 h and a smaller one shortly after dusk are evident (Fig. 6B).

Sebastes flavidus also appears to show a diel periodicity in its feeding pattern (Fig. 7). The fullness and digestion scores track each other very closely and show distinct peaks of feeding intensity around noon and shortly after dusk, although the number of samples in the latter period was limited (Fig. 7A). The actual mean weight ratio showed similar trends, but the noon peak is somewhat obscured (Fig. 7B). The percentage of empty stomachs was highest in the morning and remained low through the remainder of the day unlike that found for *S. pinniger*.

A high degree of variability in the mean weight ratio was found several times, especially during periods of peak feeding when both totally distended and almost empty stomachs were often found together. The differences in the weight

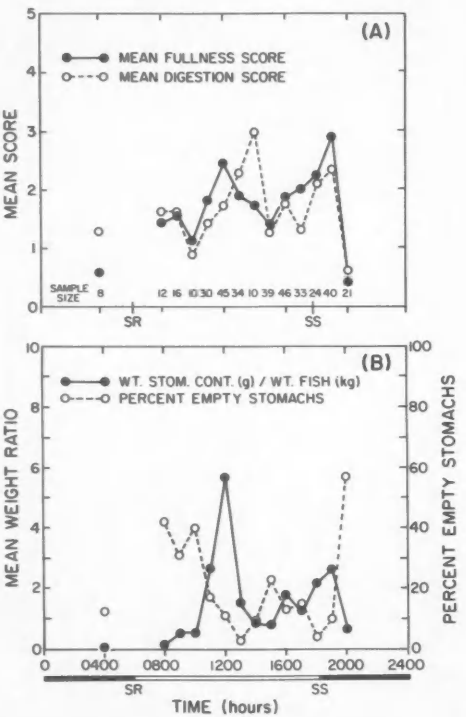

FIGURE 6.—Feeding intensity indices for *Sebastes pinniger* at adjusted times of the day. See text for explanation of indices.

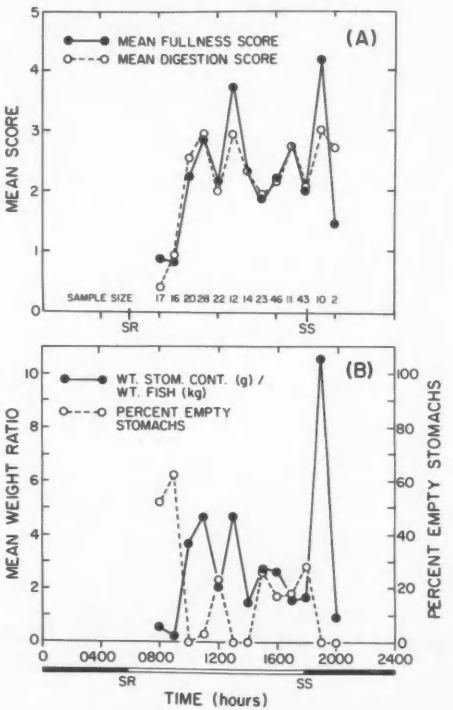

FIGURE 7.—Feeding intensity indices for *Sebastes flavidus* at adjusted times of the day. See text for explanation of indices.

ratios at the individual times were subjected to an analysis of covariance which compared the weight ratios adjusted for fish size (Jenkins and Green 1977). Both *S. pinniger* ($F_{(12,354)} = 5.68$, $P < 0.001$) and *S. flavidus* ($F_{(11,262)} = 6.51$, $P < 0.001$) showed significant differences in the mean weight ratios over the times tested, implying that feeding varied during the diel period. No significant differences ($P > 0.05$) in stomach fullness were associated with size or sex of the predator for either species.

Predator-Size Variation

The proportion of empty *S. pinniger* stomachs as well as the percent frequency of occurrence and percent weight of prey taxa were remarkably invariant among the four predator size classes (Table 14). Only the largest size class (≥55+ cm) shows any substantial variation with a larger proportion by weight of fishes and a commensurate decrease in weight of euphausiids consumed. Much of this fish weight was contributed by a few individual fish of large relative size (mostly adult *S. jordani*); the frequency of occurrence of fishes is only slightly higher for this largest size class.

Few obvious size-related trends were apparent for *S. flavidus*. The two smallest size classes consumed the largest proportion of euphausiids. *Euphausia pacifica* were less important for large fish. Decapods and cephalopods showed similar trends except that the frequencies of occurrence were highest for cephalopods but lowest for decapods in the largest size class. Fishes were consistent in their weight and occurrence proportions except that one size class (40-<45 cm) had much lower proportions than the others. Few trends were apparent for either amphipods or gelatinous zooplankton although both groups were commonly found.

To determine if different sizes of rockfish selected different sizes of prey, all fish that contained measurable prey were grouped into 10 mm length intervals and the means and ranges of their prey were plotted against fish size (Fig. 8). Although some exceptions exist, the majority of the prey of *S. pinniger* are found within a narrow range of prey sizes, a range (15-27 mm) largely determined by adult euphausiids, the dominant prey category (Fig. 8). Fishes of the largest two size classes consumed larger prey on average, and their prey had the largest variation in size due to high numbers of both small and large prey consumed by these fish. No significant relationship was found between length of fish and either overall size of prey or size of euphausiid prey.

Sebastes flavidus showed a much greater range in the sizes of prey consumed with the variation and range in prey length increasing with size of predator (Fig. 8). The mean size of prey eaten did not appreciably increase until the very largest size classes. Although the maximum prey size increases with fish size, the minimum size varies little throughout the length ranges examined. Again for this species, no relationship was found between fish length and overall or euphausiid prey lengths.

The size distribution of prey is shown for both species in Figure 9. The prey-size spectrum of *S. pinniger* was distributed fairly normally with the

TABLE 14.—Variation in major prey taxa composition with size of predator for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % *W* = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Size range (cm)	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
<45	64 (17.2)	48.4	43.2	21.9	9.7	68.7	91.4	4.7	3.1	6.2	0.3	—	—	14.1	4.8	4.7	0.4
45-<50	102 (17.6)	51.8	46.1	17.6	18.6	67.6	92.5	4.9	0.9	4.9	0.1	—	—	13.7	6.5	5.9	0.1
50-<55	146 (14.4)	47.3	65.6	21.2	12.0	61.1	94.9	5.5	0.2	4.1	+	—	—	11.0	4.7	8.9	0.1
≥55	56 (14.3)	58.9	49.3	12.5	7.6	67.9	83.4	5.4	0.2	7.1	+	—	—	16.1	16.3	14.3	0.2
Sebastes flavidus																	
<40	35 (0.0)	88.6	44.7	57.1	11.7	94.3	61.3	11.4	0.1	14.3	0.1	14.3	2.8	31.4	34.6	2.9	0.1
40-<45	61 (22.9)	45.9	50.2	29.5	12.4	52.5	83.9	13.1	1.2	24.6	0.2	13.1	8.4	9.8	5.8	4.9	0.4
45-<50	126 (21.4)	47.6	22.9	38.1	13.7	57.1	46.8	11.1	3.7	12.0	0.1	12.7	17.4	29.3	29.3	7.9	2.4
≥50	42 (2.4)	47.6	25.8	30.9	8.3	54.7	51.9	7.1	2.6	23.8	0.3	21.4	13.6	45.2	30.3	21.4	0.1

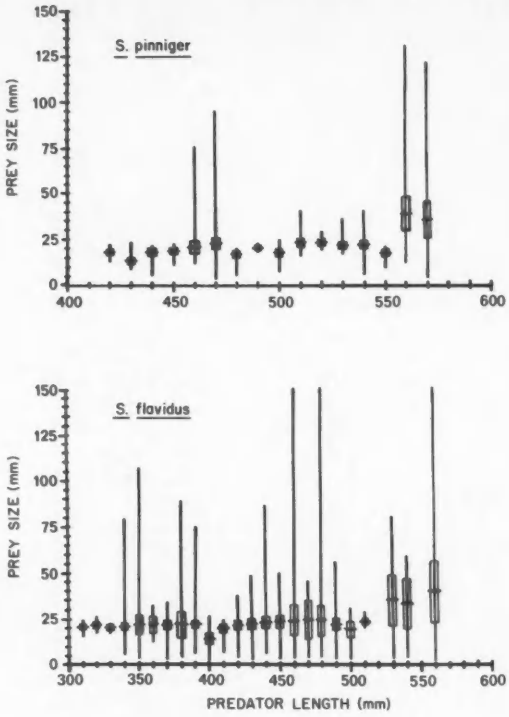

FIGURE 8.—Mean (horizontal lines) ±95% confidence limits (boxes) and ranges (vertical lines) of prey sizes found for each 10 mm interval of *Sebastes pinniger* and *S. flavidus*.

mode coinciding with the mean ($\bar{x}$ = 10.38 mm), although disjunct groups of small and large prey were found (Fig. 9). The prey-size spectrum of *S. flavidus* was slightly skewed toward the larger sized prey with the mean size ($\bar{x}$ = 18.44 mm) less than the mode. A smaller peak also appeared around 25 mm. No significant differences were found in the mean prey sizes utilized by the two species (Student's *t*-test, $P > 0.05$).

Analysis of Variation

The results of the chi-square analyses for *S. pinniger* showed that none of the factors analyzed had a significant effect on the occurrence of food in the stomachs (Table 15). At least one of the factors was related to the occurrences of all seven prey categories examined. Seasonal effects were the most significant (all $P \leq 0.01$) and were due to the higher occurrences of hyperiid amphipods, fishes, and gelatinous zooplankton in fall and winter. Area and time of capture showed both highly significant ($P \leq 0.001$) and insignificant effects depending on the prey category, but most comparisons were significant at the 0.05 level. In none of the prey categories examined did the size of the predator have a significant effect on the relative proportions consumed.

For *S. flavidus*, season of capture and size of predator affected the proportion of empty stomachs found (Table 15). Again season had the most significant influence on prey occurrence and was significant in all eight prey categories. Highly significant differences were found in area of capture and size of predator especially in the euphausiid and fish categories. Differences in occurrence of prey with time of capture deviated from expected the least of all the factors analyzed.

DISCUSSION

The five species of rockfishes examined rely heavily, if not exclusively, on pelagic macrozooplankton and micronekton. Although some benthic species appear in the prey lists (e.g., *Lyopsetta exilis*, *Munida quadrispina*, *Psettichthys melan-*

TABLE 15.—Results of chi-square analyses testing for differences in the occurrence of food and specific prey categories within the various factors. All significances are with three degrees of freedom except where noted.

Factor analyzed	Occurrence of food	*Euphausia pacifica*	*Thysanoessa spinifera*	Total euphausiids	Decapods	Amphipods	Cephalopods	Fishes	Gelatinous zooplankton
Sebastes pinniger									
Season	6.59	23.09***	72.48***	11.26**	113.28***	16.76***	—	15.87***	39.96***
Area[1]	0.19	8.61*	5.22	11.42***	0.46	22.44***	—	7.95*	35.66***
Time	4.32	28.18***	53.77***	11.86**	1.37	13.05***	—	1.43	19.21***
Size	0.67	3.12	3.24	6.26	0.04	0.98	—	1.26	4.35
Sebastes flavidus									
Season[1]	9.79**	13.32***	51.33***	10.02**	30.27***	11.15***	6.65*	21.43***	11.67***
Area	5.76	20.83***	15.81***	14.23***	1.21	2.76	11.62**	22.41***	6.43
Time	1.12	3.21	5.42	2.38	10.43*	12.30**	8.25*	9.33*	5.60
Size	17.50***	13.78***	6.35	14.17***	2.02	11.69**	0.94	12.92***	8.86*

* = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.
[1]Significance with two degrees of freedom.

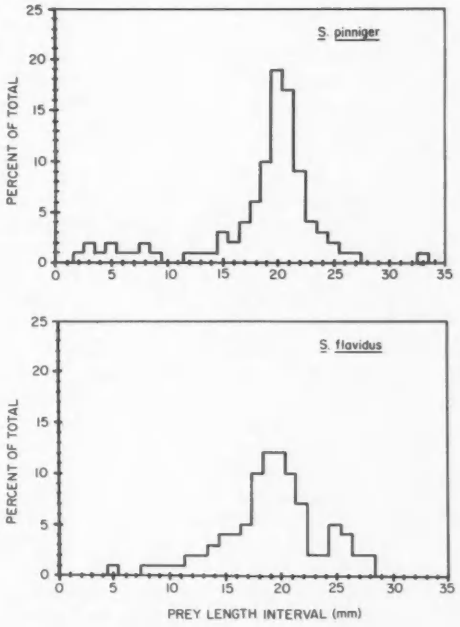

FIGURE 9.—Prey size spectra in percent for *Sebastes pinniger* and *S. flavidus*.

ostictus), they were represented by postlarval or juvenile forms commonly found in the plankton. Several comparatively large nektonic fishes and cephalopods (e.g., *Clupea harengus pallasi*, *Sebastes jordani*, *Loligo opalescens*) were eaten, but their occurrences were relatively rare. Conversely, the virtual absence of many common benthic and epibenthic organisms of appropriate size such as mysids, cumaceans, and gammaridean amphipods further implies that these fish do not normally feed on benthic animals.

These findings concur with the limited number of previous studies dealing with food habits of offshore rockfish. Phillips (1964) reported on the diet of all the species included here except *S. alutus*. Although little taxonomic detail and no quantitative data on prey consumption were given, euphausiids were listed as important forage items for all four species. Fishes were also important prey for several species, especially *S. flavidus*. Skalkin (1964), in a study of *S. alutus* in the Bering Sea, found mostly euphausiids and copepods in the stomachs, but also stated that a few nektobenthic species and "fragments" of benthic echinoderms were present.

The food habits of *S. flavidus* have been described in several studies off Oregon and Washington. Pereyra et al. (1969) found unusually high abundances and volumes of the mesopelagic fish, *Stenobrachius leucopsarus*, in *S. flavidus* stomachs collected near Astoria Canyon and hypothesized that local hydrographic conditions may have aggregated these prey at high densities. Gunderson et al. (1980)[5] reported that *S. flavidus* off the coast of Washington fed mostly on fishes, including some pleuronectid fishes possibly eaten near the bottom along with benthic polychaetes. Lorz et al. (1983) found euphausiids dominating the diet of *S. flavidus* off Washington and Queen Charlotte Sound, with fishes of greater importance in the latter region. Another deepwater species, *S. marinus*, found in the North Atlantic Ocean, also fed chiefly on pelagic prey (Lambert 1960). Euphausiids, hyperiid amphipods, and copepods were the most abundant prey, but mesopelagic fishes were also found in large numbers.

Among the species considered here, two divergent feeding patterns are apparent, assuming that

[5]Gunderson, D. R., G. L. Thomas, P. Cullenberg, D. M. Eggers, and R. Thorne. 1980. Rockfish investigations off the Washington coast. Ann. Rep., prep. for NMFS, Univ. Wash., 68 p.

the same prey items are equally available to all species. These can be seen most clearly in the divergence of the cumulative curves of the number of prey species (Fig. 2). Three species (*S. pinniger*, *S. alutus*, and *S. crameri*) tend to be stenophagous, with very few prey items represented in large volumes of prey organisms. Euphausiids appear to be the most sought after or available prey, and other prey taxa occur in low numbers. These three species show similar low food breadth values.

Sebastes flavidus and *S. diploproa*, on the other hand, have steadily rising prey curves that continue to rise and approach an asymptote beyond the limits of the figure. These curves are characteristic of euryphagous predators which show high overall prey diversity as well as high within-stomach diversity. This high prey diversity can be seen in the greater food breadth values attained by these two species. Although euphausiids predominate in these stomachs, high abundances of other prey, which may be preferred but have lower abundances and availabilities than euphausiids, also occur.

The diet overlap measurements calculated here may be useful in comparing how similar the food habits of two species are but may be of limited use when interpreted in an ecological sense. The interaction of factors that affect or determine the diet of a particular species is complex and may include such factors as temporal and spatial distribution of prey, behavioral adaptations of predator and prey, prey detection capabilities, and feeding morphologies of predators (Hyatt 1979). Caution should be exercised when inferences are made about possible species interactions based on diet overlap measurements alone. Two species may have broadly overlapping diets in terms of prey composition but segregate with respect to prey sizes selected, time of feeding, or habitat utilization (Schoener 1974; Ross 1977; Werner 1979; Macpherson 1981).

Sebastes pinniger and *S. flavidus* are two of the most abundant rockfish species within the geographical confines of this study. They inhabit similar depth ranges, latitudinal ranges, and show broadly overlapping areas of peak abundances according to trawl survey data (Alverson et al. 1964; Richardson and Laroche 1979; Gunderson and Sample 1980). Adams (1980) found that these two species had the highest positive association in trawl catches using presence-absence data of the seven abundant species he examined. Little is known, however, about their small-scale horizontal and vertical distribution. Although they may occupy similar bottom habitat, *S. flavidus* may be more pelagic (Alton 1972).

Seasonal, geographical, and diel variations in the abundance and availability of the important prey of *S. pinniger* and *S. flavidus* could be a major cause of the variations in the diet of these species. These variations may be the result of intrinsic prey population fluctuations with season, behavioral adaptations such as diel and ontogenetic vertical migration, or may stem from the prevailing oceanographic conditions either concentrating, dispersing, or transporting prey so that all prey are not equally available in the limited time and space frame of the individual predator. Current patterns alone are known to vary with season, depth, and geographic area (Huyer et al. 1975; Ingraham and Love 1978) and may affect the availability and concentration of prey.

Quantitative estimates of the seasonal and areal distributions of the total prey spectrum consumed by these rockfishes are limited. Day (1971) sampled macrozooplankton and micronekton from the northern part of the range of this study (lat. 46°45'-50°02'N) using a 0.9 m Isaacs-Kidd midwater trawl in the upper 150 m of the water column during the spring and fall. He found a peak in the biomass of catches at the outer edge of the continental shelf. Euphausiids dominated the catch at most stations, and *E. pacifica* and *T. spinifera* together accounted for 90% of the total abundance of all organisms collected, which is similar to the abundances found in the stomachs of several species examined here. Although the proportional abundance of *E. pacifica* varied greatly relative to *T. spinifera*, *E. pacifica* dominated the catches and was most concentrated during the spring when it comprised the largest proportion of the stomach weights in our study. Mesopelagic fishes were commonly collected in Day's sampling, but mostly at the offshore stations.

Pearcy (1972) reviewed the species composition, vertical and horizontal distribution, and variations in abundance of the macrozooplanktonic and nektonic fauna derived from 8 yr of sampling off Oregon. Annual and seasonal changes in the abundance and distribution of many species could be correlated with changes in oceanographic conditions. Following the cessation of upwelling in fall, surface waters flow predominantly inshore and northward, transporting shrimps and myctophids onto the shelf. We found that shrimp and myctophids became more important in the diets of

S. pinniger and *S. flavidus* at this time. An inshore-offshore peak in the biomass of midwater collections occurred on the edge of the continental slope off the central Oregon coast (lat. 44°39′ N), a zone where oceanic macrozooplankton and micronekton may be concentrated by advection (Pearcy 1976). This is the region where pelagic-feeding rockfishes are often concentrated (Gabriel and Tyler 1980).

The majority of the prey species found in the stomachs of the rockfish species examined are pelagic species that undertake extensive diel vertical migrations and are important components of the biological sound scattering layer in the Northeast Pacific (Pearcy and Laurs 1966; Brinton 1967; Pearcy and Mesecar 1971; Pearcy 1972; Alton and Blackburn 1972). In this study, both of the euphausiid species of interest, *E. pacifica* and *T. spinifera*, have been found to have substantially different daytime and nighttime vertical distributions. According to Alton and Blackburn (1972), catch rates of *T. spinifera* off the coast of Washington were the highest near the bottom during the early evening hours (1800-2000 h) and at the surface a few hours later (2100-2300 h).

The diurnal downward migration of these organisms over the continental shelf may result in a substantial biomass in close proximity to near-bottom predators, such as rockfishes, which feed on pelagic prey during the day. Deeper migration to daytime depths typical of their more open ocean conspecifics is restricted by the shelf, especially in shoaler areas such as Heceta Bank. Isaacs and Schwartzlose (1965) found dense populations of predators, including many rockfishes, on shallow banks off California; these predators presumably take advantage of net inshore transport by currents of oceanic organisms over the bank. Pereyra et al. (1969) reported high incidences of predation on mesopelagic organisms by aggregations of *S. flavidus* residing on the shelf edge near a deep canyon. Vertically migrating mesopelagic organisms may also constitute an important food source for many species of slope fishes (Sedberry and Musick 1978).

Diel vertical distribution patterns of offshore rockfishes are not well documented. Based on acoustic observations, Westrheim (1970) concluded that schools of Pacific ocean perch move off bottom at night. Pereyra et al. (1969) and Love (1981) caught rockfishes that were apparently feeding well off the bottom at night. Lorz et al. (1983) concluded that *S. flavidus* off Washington fed on euphausiids during night or early morning hours, when these euphausiids would be expected to be in surface waters. Similar migrations were seen on Heceta Bank during this study. Figure 10 shows an acoustic 33 kHz transect taken across Heceta Bank during the late morning (about 1023-1050 h PST). Many large "spikes" of fish aggregations were apparent extending over 100 m above bottom. Some of these were probably caused by rockfish ascending in the water column to feed. Figure 11 is a 33 kHz echogram on Heceta Bank made around 1800 h PST. The "haystacks" shown are characteristic of tight aggregations of *S. pinniger* just above bottom (Barss[6]) and may represent feeding aggregations. Also visible in this echogram is more diffuse scattering in the water column (20 m off bottom) probably caused by euphausiids. The tow made concurrently with this trace did yield a large catch of rockfish (97% *S. pinniger*), most of which had stomachs full of fresh euphausiids. This stratification of large sound scatterers below diffuse midwater scattering prey was often observed during the acoustic surveys. Atlantic cod appear to interact with pelagic prey in a similar fashion (Brunel 1965; Pearcy et al. 1979; Falk-Peterson and Hopkins 1981).

The two primary species examined in detail in this study appear to forage mainly during the midday and evening dusk periods, although sampling was limited during nighttime. The similar diel patterns of feeding intensity suggest that temporal partitioning of feeding time is not occurring between *S. pinniger* and *S. flavidus*. The differing utilization patterns of euphausiids and fishes seen for the two species (Table 13) may be related to the vertical positioning of the two species in the water column. *Sebastes flavidus* may feed high in the water column, prey upon adult herring and pelagic juvenile fishes during the daytime, and intercept euphausiids during crepuscular periods, whereas *S. pinniger* may stay nearer the bottom where they may feed almost exclusively on increased daytime aggregations of euphausiids.

The occurrence of a high percentage of empty stomachs and generally low feeding intensity indices in *S. alutus*, which were caught mainly in late afternoon in our study, suggests that this species is more nocturnal in its feeding patterns, assuming that this species has similar regurgita-

[6]W. Barss, fishery biologist, Oregon Department of Fish and Wildlife, Newport, OR 97365, pers. commun. December 1980.

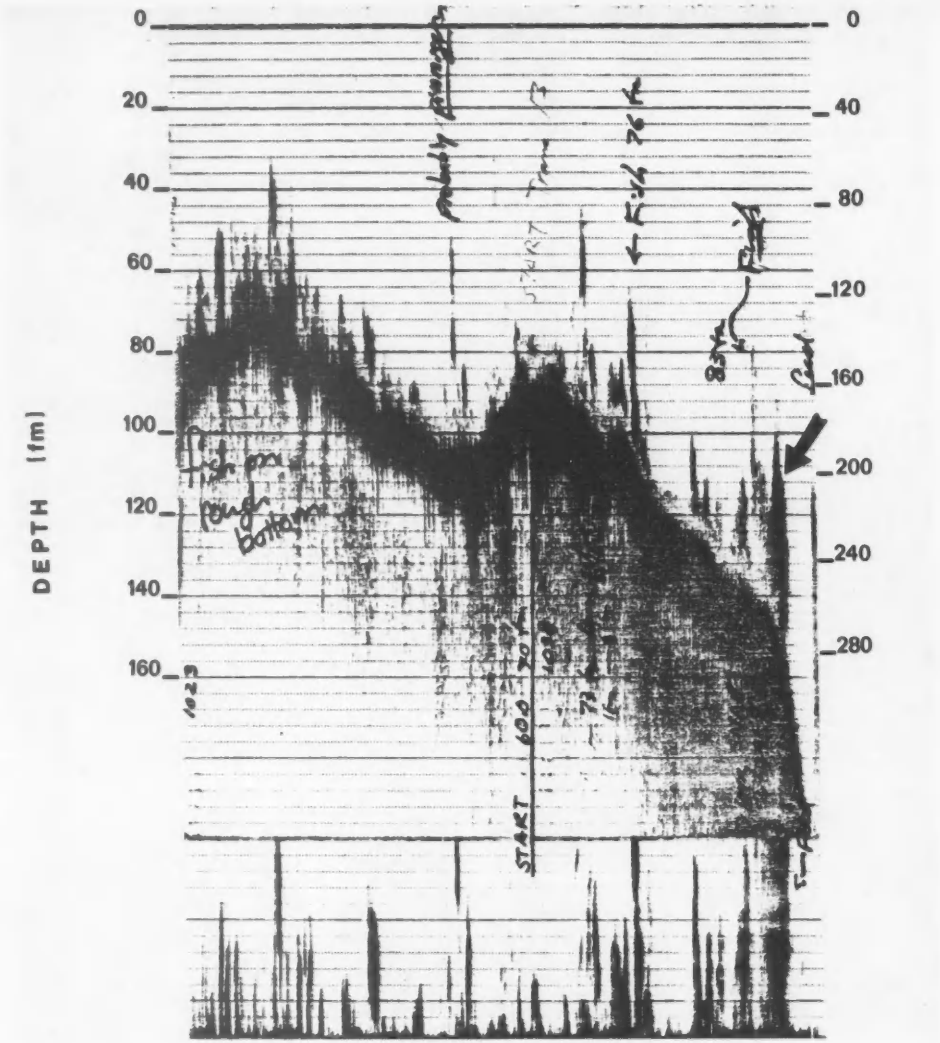

FIGURE 10.—Echo sounder (Krupp-Atlas Elektronik Model 611, 33 kHz) transect across Heceta Bank showing characteristic rough topography and schools of fish in the water column. The larger signal at the extreme right (arrow) is believed to be a large concentration of forage fish, possibly myctophids. The bottom section of the figure shows an expanded version of the layer just above the seabed.

tion and digestion rates as the other species studied. Skalkin (1964) found that the feeding intensity of immature *S. alutus* in the Bering Sea was highest around midday with a smaller peak shortly after dusk as found for *S. pinniger* and *S. flavidus* in this study. He also hypothesized that larger fish may feed higher in the water column at night on euphausiids, but his nighttime sampling was also limited. Similar pelagic feeding by *S. alutus* at night may be occurring in our study area, but these fish would not be available to bottom trawls at this time.

The rockfishes considered here are just a few species in an extensive guild (sensu Root 1967)

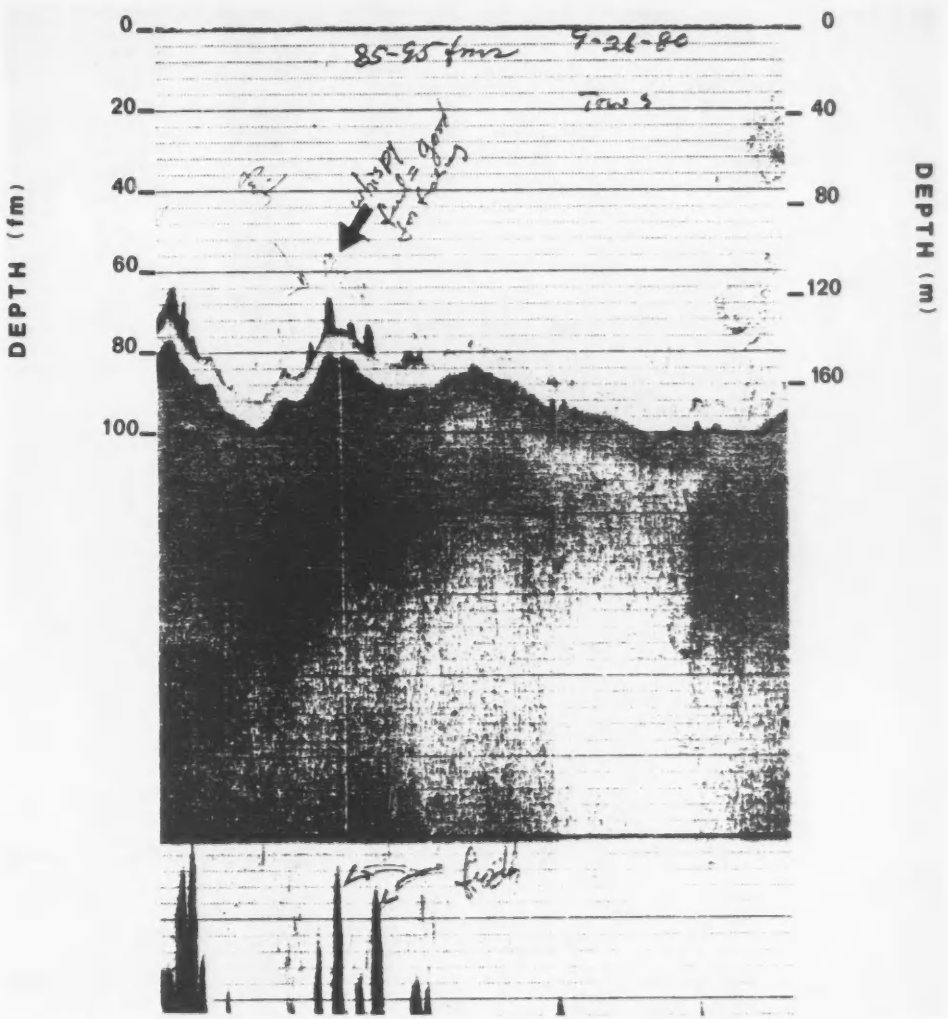

FIGURE 11.—Smoother bottom profile made during a tow showing the "haystacks" of rockfish in close association with the bottom and possibly preying upon the food organisms (arrow) directly above them.

of organisms which feed in varying degrees on euphausiids. Other pelagic predators in this study area known to feed intensively on euphausiids include Pacific hake (Alton and Nelson 1970), myctophids (Tyler and Pearcy 1975), juvenile salmon (Peterson et al. 1982), and squid (Karpov and Cailliet 1978). Standing stocks and production rates of euphausiids in northern latitudes may be of such magnitude that many predators often subsist on them in coexistence rather than compete for other more limited resources. More research is needed on the biology and distribution of these abundant prey species and their importance to fishery resources. In complex, multispecies fisheries such as those utilizing rockfishes, it may be possible to treat several species with similar

life histories and which prey on similar resources as a biological unit for management purposes.

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SPECIES ASSOCIATIONS AND COMMUNITY COMPOSITION OF MIDDLE ATLANTIC BIGHT CONTINENTAL SHELF DEMERSAL FISHES[1]

J. A. COLVOCORESSES and J. A. MUSICK[2]

ABSTRACT

Cluster analyses of seasonal NMFS Groundfish Survey bottom trawl catches on the Middle Atlantic Bight continental shelf revealed consistent species associations and faunal zones over a 9-year period. Boundaries between faunal zones tended to follow isotherms and isobaths. During the late winter-early spring, the following faunal zones were found: Northern inner shelf, northern mid-shelf, southern inner- and mid-shelf, and outer shelf-shelf break. Five species groups were identified: A small cryophilic group restricted to the first zone, a cold-water boreal group found in the first two zones, a ubiquitous boreal/resident group containing the major dominants, a warm-temperate group confined to the warmer southern and outer shelf waters, and a group of slope residents confined to the deepest zone. During the fall, five faunal zones were found: Southern inner/mid-shelf, northern inner shelf, northern mid-shelf, outer shelf, and shelf break. Five species associations were largely analogous to those in the spring, with the following exceptions: The cryophilic group was absent, the ubiquitous group contained mixed boreal and warm-temperate elements, and a second outer shelf group was recognized. The most notable change in the distribution of groups from the spring was a general northward shift and a sharply defined inshore movement of the temperate group.

Communities of fishes on the continental shelf have rarely been studied beyond the compilation of species lists for given areas. This is enigmatic when one considers the large amount of survey data that has been collected from much of the world's continental shelf waters in connection with fishery exploration and monitoring. While trawl survey data have traditionally been collected with the primary aim of assessing commercially harvestable stocks, they also provide an excellent base for evaluating the interspecific relationships among trawlable organisms.

The few studies which have previously addressed community structure of open continental shelf fishes have found clearly definable species associations with distributions related to environmental parameters. Demersal fish species assemblages found using objective mathematical measures have been described for the continental shelves in the Gulf of Guinea (Fager and Longhurst 1968), northwest Pacific coast of the United States (Day and Pearcy 1968), and Campeche Bank off Mexico (Sauskan and Ryzhov 1977).

Since 1967 the National Marine Fisheries Service (formerly Bureau of Commercial Fisheries) has conducted a semiannual bottom trawl survey of the continental shelf waters from Nova Scotia to Cape Hatteras (Grosslein 1969). This program has produced a data base which offers a unique opportunity for the analysis of the composition and variability of the fish communities in this region.

In the present study, that portion of these data collected in the Middle Atlantic Bight (Cape Cod to Cape Hatteras) during the cruises from fall 1967 through spring 1976 were analyzed with the aim of defining the composition of fish communities present within this area and how they vary geographically, thermally, and seasonally.

METHODS

Sampling

Groundfish Survey cruises were conducted by the National Marine Fisheries Service during the fall and spring from fall 1967 through spring 1976, aboard either the RV *Albatross IV* or RV *Delaware II*. The survey area extended from the 15-fathom (27 m) contour offshore to 200 fathoms (365 m). A stratified random sampling design was utilized, based on depth and geographical zones (Fig. 1). Catch data from strata 1-12 and 61-76 (Middle Atlantic Bight) were analyzed in the present study. Sampling intensity in each stratum was allocated according to the geographic area of each stratum

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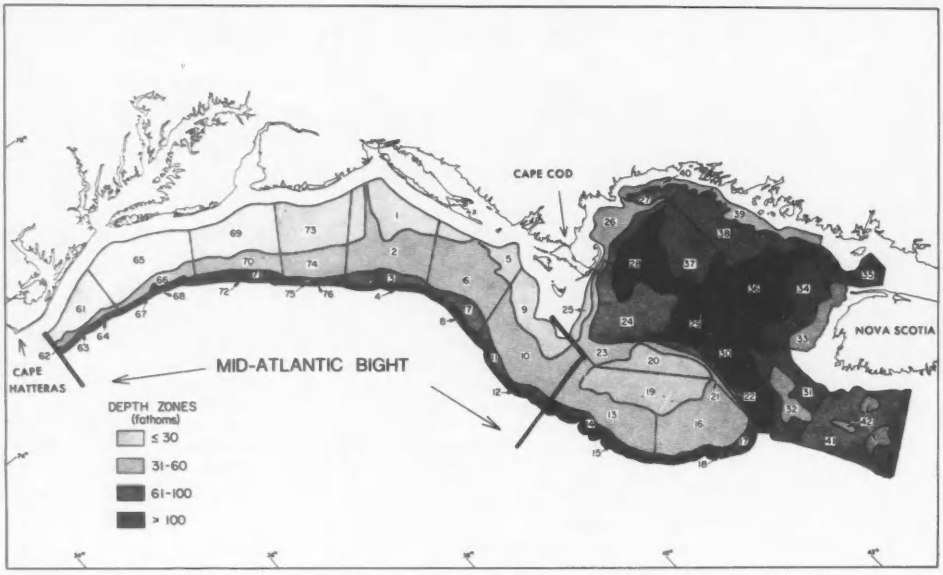


FIGURE 1.—Northwest Atlantic area sampled by NMFS Groundfish Survey. In the present study, data collected from the Middle Atlantic Bight area (strata 1-12, 61-76) between fall 1967 and spring 1976 were examined.

(2-16 stations per stratum). At each station a tow of ½-h duration at a speed of 3.5 kn was made along the bottom. A standard #36 Yankee trawl was utilized except during the spring cruises from 1973 to 1976, when a modified high-opening #41 Yankee trawl was used. The fishes captured were identified, counted, and weighed by species. A bathythermograph cast was made at each station. Further details of sampling design and sample processing may be found in Clark and Brown (1977) and Grosslein (1969).

Analyses

Clustering

Catch data were initially analyzed separately for each of 18 cruises, using numerical classification (clustering). Assemblages of fishes were defined by computing a similarity coefficient, $S_{(j,k)}$, among species from the species-station matrix and subsequently classifying species into clusters or groups (Sneath and Sokal 1973). Stations were clustered in the same manner from the inverted matrix, and species and station (site) groups were compared by nodal analysis (Lambert and Williams 1962). Matrix values entered were counts of individuals, as biomass measurements are overly influenced by the presence of relatively rare but large, motile fishes (which are poorly sampled by trawls) in the collections.

The similarity coefficient used was the Canberra metric (Lance and Williams 1967), which is particularly effective when the organisms under study are contagiously distributed (Clifford and Stephenson 1975) as most fishes are. Also, to further reduce the effects of contagion, the numerical abundance data were transformed [$\log_{10}(x + 1)$] before analysis (Taylor 1953). Species were eliminated from cluster analysis if they occurred at $<5\%$ of the stations occupied during a sampling period. Although this is a more severe data reduction than is commonly employed, examination of the raw matrix and trial runs at various cutoff levels indicated that species occurring below this level showed highly inconsistent distributions.

The clustering strategy used was flexible fusion with beta set at the conventional value of -0.25 (Boesch 1977). Calculations were performed on an IBM 370-115[3] at the Virginia Institute of Marine Science using the Fortran IV program COMPAH

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

(Combinatorial Polythetic Agglomerative Hierarchical Program) developed at the institution. Output was in the form of similarity matrices and computer generated dendrograms.

The choice as to which branches in the dendrograms were to be identified as biologically significant groups was based on the following procedure. Each branch of the dendrogram, composed solely of fusions involving only one entity as at least one-half of each fusion, was considered to constitute a minimal grouping. The distribution of each minimal grouping was then map-plotted, with logarithmic keyed symbols being used for plots of abundances of minimal species groupings. The plot of each grouping was then compared with that of the grouping with which it next fused; if no significant differences in distribution were evident, the fusion was considered to be intragroup. This procedure was repeated until all minimal groupings had been fused into groups showing evident distributional differences. In cases where there was any doubt as to whether two groups should be fused, nodal analysis diagrams were generated and compared for the two cases and the decision producing the "crisper" result (Clifford and Stephenson 1975) utilized. While this method obviously involves some subjectivity in the recognition of groups, it has been pointed out by several authors that all methods of interpreting numerical classifications require a certain degree of subjectivity and that fixed stopping rules are especially inappropriate with fusion strategies which introduce a group size-dependent element into intergroup relative affinities (Boesch 1977; Pielou 1977; Clifford and Stephenson 1975).

Two methods of nodal analysis were performed. The patterns of "constancy" and "fidelity" of species groups to site groups were expressed as relative densities of cells of a two-way table (Stephenson et al. 1972). Constancy is the proportion of the number of occurrences of each species group in the site group to the total number of occurrences possible (Boesch 1977). The index has a value of 1 when all members of a species group occur in all collections in a site group and a value of 0 when a species group does not occur in a given site group. Fidelity is a measure of the degree to which species groups are limited to site groups. The fidelity index used in this study was the constancy of a species group within a site group divided by the average constancy over all site groups. This index is unity when the constancy of a species group in a site group is equivalent to its overall constancy, >1 when its constancy in the site groups is greater than that overall, and between 0 and 1 when its constancy is less than its overall constancy. A chi-square test was applied to the fidelity value of each cell to determine whether it varied significantly ($\alpha = 0.05$) from 1. Fidelity values significantly >1 indicate a positive association of species in a group with a site group, while values significantly <1 suggest a "negative" association. In the present analyses, a highly positive (or strong) association was inferred if the number of occurrences of a given species group within a site group was twice that necessary to produce a fidelity value significantly >1, and a highly negative association was assumed when the number of occurrences was less than half that necessary to produce a fidelity value significantly <1. All nodal diagrams were drawn with the width of the rows and columns proportional to the number of entities in the respective site and species groups.

Species Dominance

Numerically dominant species have been used by ecologists for many years to characterize communities (Thorson 1957), and changes in dominant species often reflect faunal changes. In the present study, we have compared patterns of species dominance among site groups. A species was included in dominance comparisons if it occurred among the five most abundant species in at least 20% of all the stations from a site group.

Faunal Affinities

The faunal affinities of fishes captured were determined by examining published records of their usual ranges of occurrence (Bigelow and Schroeder 1953; Leim and Scott 1966; Struhsaker 1969; Musick 1972). Most warm-temperate species had resident populations south of Cape Hatteras in the "Carolinian" faunal province (Hazel 1970) and had their normal northern range limit somewhere within the Middle Atlantic Bight south of Cape Cod. Boreal species had permanent populations north of Cape Cod, and most had their southern range limit somewhere within the Middle Atlantic Bight north of Cape Hatteras. A few boreal species transcend Hatteras through bathymetric submergence. Certain components of the fauna tended to be residents on the inner shelf (*Scophthalmus aquosus*) or outer shelf (*Paralichthys oblongus*). Many species were resident on the shelf edge and upper slope (Musick 1976).

Pooling of Within-Season Cruises

Size of the data matrix was too large for simultaneous clustering of either of the two multiple-year seasonal data sets. However, the results of the cluster, nodal, and dominance analyses of the individual cruises revealed a high degree of within-season repetition in the composition and distribution of species groups and in the faunal, geographic, and hydrographic attributes of site groups. Major repetitive species groups were recognized for each season, and site groups for each year were referred to generalized seasonal site groups. The validity of these groups was examined by subjecting the pooled seasonal data sets to nodal and dominance analyses based on these groupings and comparing these results to those for the individual cruises.

RESULTS AND DISCUSSION

Thermal Regime

The geographic patterns of bottom-water temperatures were variable among years within both of the sampling seasons, although these differences were minor compared with the seasonal variation within a given year. Variability among years within a season can be attributed to two sources: Climatic differences among years and sampling artifacts (i.e., differences in the dates and duration of the sampling periods, and stochastic differences arising from the location of stations and the temporal sequence in which they were done).

The spring cruises were conducted in March and April, the period during which water temperatures in the Middle Atlantic Bight are at a mini-

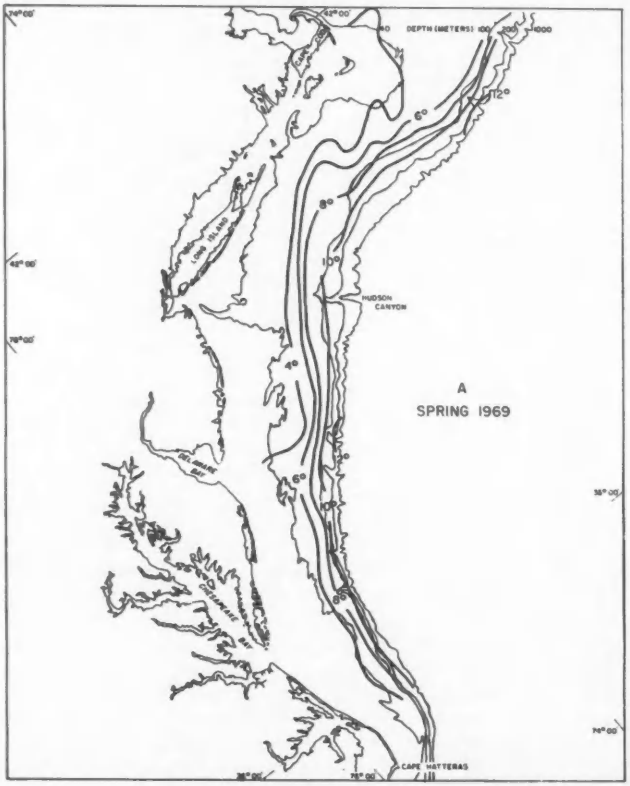
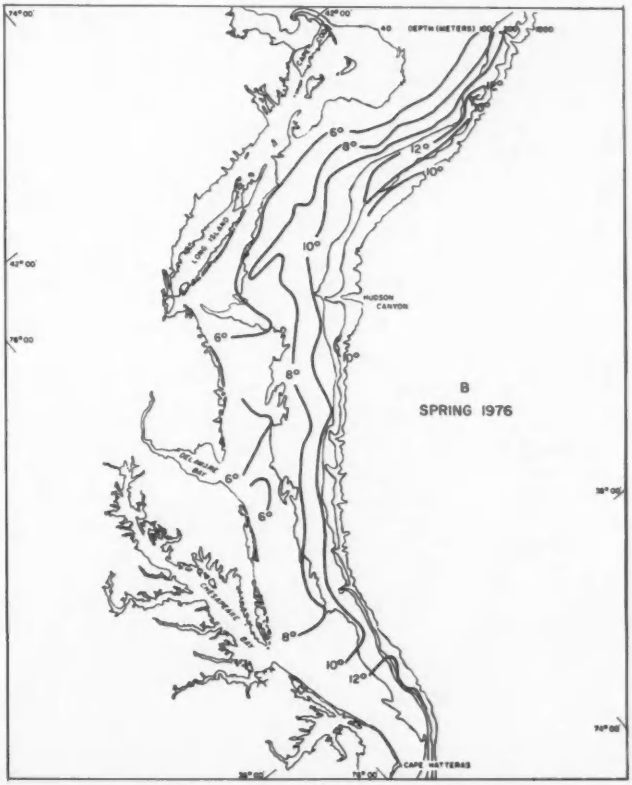


FIGURE 2.—Bottom isotherms for spring 1969 (A) and 1976

mum (Walford and Wicklund 1968), and therefore it is more appropriate to consider these cruises as having sampled the late winter distribution of fishes (Musick and Mercer 1977). There was a definite trend toward warmer temperatures during the study period for this season which cannot be completely attributed to sampling artifacts (Davis 1979). Bottom isotherms extrapolated from the collection data are shown for two cruises representative of the warmer (1976) and cooler (1969) extremes (Fig. 2). During the 1969 cruise, inshore and mid-shelf temperatures were <4°C north of Delaware Bay and between 4° and 6°C between Delaware Bay and Cape Hatteras, with an increasing gradient present along the entire outer shelf. In 1976 temperatures of <6°C were encountered only at northern inshore stations. South of Chesapeake Bay there was a southwardly increasing thermal gradient perpendicular to the shoreline, and the outwardly increasing gradient was distributed across a greater portion of the shelf. Bottom temperatures for the other spring cruises exhibited patterns intermediate between these two (Davis 1979).

Fall sampling cruises were conducted primarily in October. Because of water column turnover, this is the time of maximum temperature for mid-shelf bottom waters in this region (Bigelow 1933); however, coastal waters undergo rapid cooling during the fall (Parr 1933), initiating migrations for many fishes that spend the summer inshore. Bottom isotherms for a typical warm (1973) and cool (1971) fall sampling period are shown in Figure 3. In 1971 a strong thermal gradient was encountered along the mid-shelf from New York to Cape Hatteras. A pocket of cooler water (6°-9°C) was present northward and offshore of this gradient, where turnover was in progress or just beginning.



(B) extrapolated from NMFS Groundfish Survey cruises.

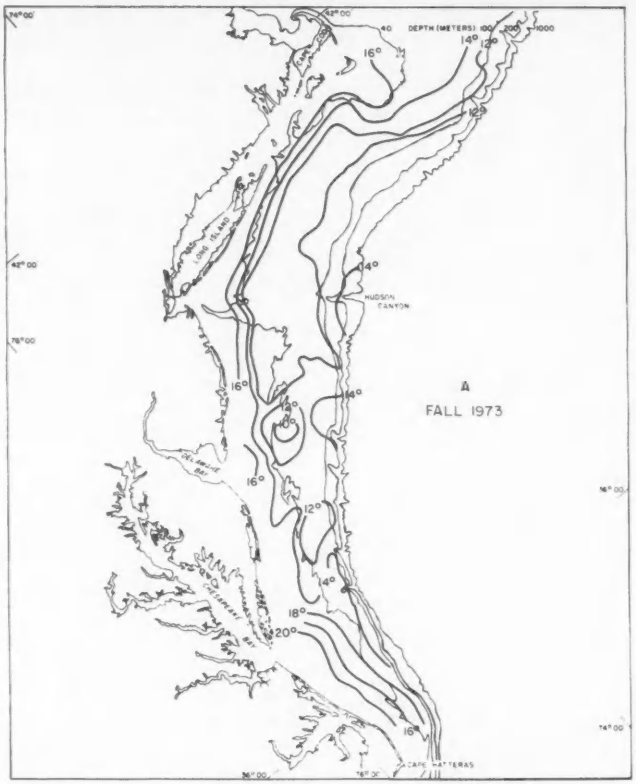


FIGURE 3.—Bottom isotherms for fall 1973 (A) and 1971

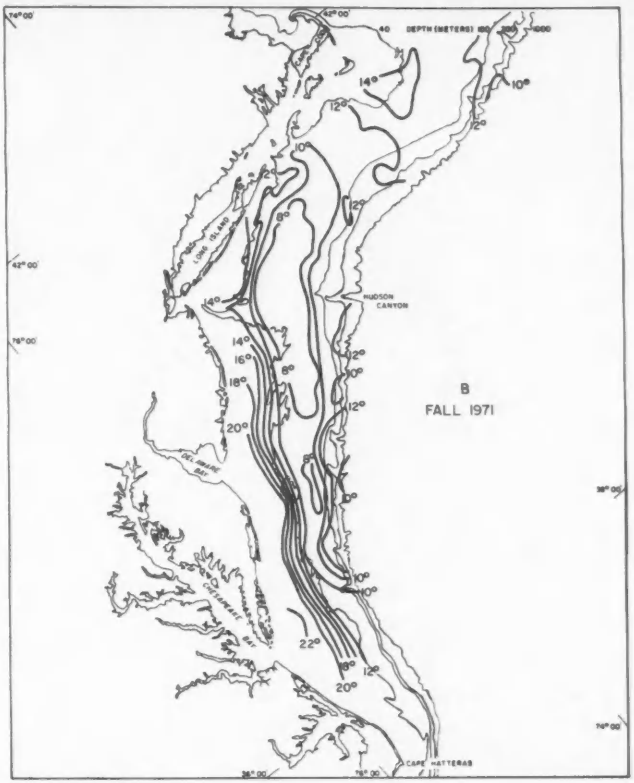
During 1973 bottom-water temperatures were less stratified and 2°-4°C warmer throughout most of the study area. Inshore temperatures exceeded 16°C along the entire Bight, with temperatures above 18°C occurring only south of Chesapeake Bay. The coolest temperatures were found again on the mid-shelf off New Jersey and Long Island, but the "pocket" was much less clearly defined and was composed of waters between 10° and 12°C, indicating that turnover had already occurred. The other fall cruises showed thermal regimes intermediate to those of 1971 and 1973 (Davis 1979).

Site Groups

Spring Cruises

Station groups based on cluster analysis were determined for the nine spring cruises (Colvocoresses and Musick 1979). Most groups were geographically contiguous and tended to be thermally and bathymetrically restricted. Site groups were not precisely comparable from one year to the next, but could, however, be categorized on the basis of faunal similarity, geographic location, bathymetry, and temperature.

During all nine cruises there was a group of site clusters of similar depth and temperature regimes which were contained between the shore and approximately the 8°C isotherm. The geographic extent of these groups varied from year to year, but generally covered the inner- and mid-shelf out to about 70 m from Cape Cod south to between Delaware Bay and Cape Hatteras, depending upon the southward extent of waters cooler than 8°C. These site groups were assigned to site group I (Fig. 4) for the pooled analyses. Adjacent to this group were



(B) extrapolated from NMFS Groundfish Survey cruises.

two other categories of groups: Northern outer shelf groups extending from the cold-water group to the shelf break (150 m) (pooled group II), and southern groups (pooled group III) which occupied the remaining shelf both outward and south of the 8°C isotherm. The boundary between these two categories was generally off the New Jersey coast, at which point there was often considerable overlap. The remaining outermost groups were located along the shelf break at depths of 150-350 m (pooled group IV).

In general, areas of geographic overlap between site groups can be related to variations in the thermal regime. For example, there is considerable overlap between groups I and III on the inner- and mid-shelf south of Delaware Bay. This area showed the greatest temperature variation among years, with group I station clusters predominating in the area in colder years and group III station clusters in warmer years. Hydrographic parameters and basic catch data for each stratum are summarized in Table 1. The hydrographic parameters (depth, temperature) within a site group are much better represented by the mean and standard deviation than by the range of values encountered. At a small percentage of stations only a few species were taken, and in cases where these species occurred within all or several strata, some misclassifications occurred. Because the incidence of these obvious misclassifications was low, they have been ignored rather than introducing an arbitrary system of reclassification. Virtually all extremely variant values of depth and temperature and strong deviation in geographic location within a site group were attributable to stations where only a few ubiquitous species were taken. Figure 5 illustrates temperature-depth envelopes for each site group. In order to reduce dis-

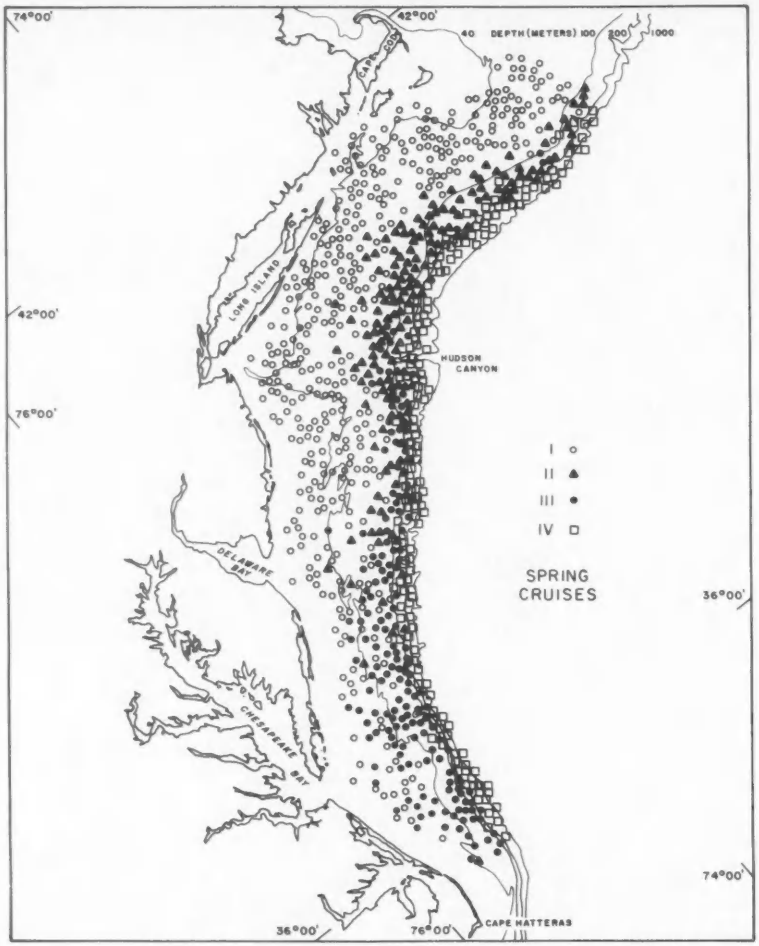


FIGURE 4.—Pooled site groups based on cluster analysis for spring NMFS Groundfish Survey cruises, 1968-76.

tortions introduced by misclassified stations, points which exceeded 2 standard deviations from either mean were not included. As may be seen by a comparison of Figures 4 and 5, groups I and IV are geographically, bathymetrically, and thermally discrete from one another with groups II and III occupying the intermediate area and somewhat overlapping the first two groups in terms of bathymetry and thermal regime. Groups II and III are largely separable on the basis of latitude (as well as faunal composition).

Fall Cruises

Station groups recognized from cluster analysis of the fall cruises (Colvocoresses and Musick 1979) were not as geographically contiguous or as thermally restricted as during the spring cruises, but could still be readily grouped into categories based on faunal attributes. During seven of the nine cruises there was a distinct southern inshore site group between shore and about 60 m extending from Cape Hatteras northward to the region off

TABLE 1.—Hydrographic and average catch parameters by site group for Spring NMFS Groundfish Survey cruises, Middle Atlantic Bight, 1968-76. The 1968-72 cruises used a #36 Yankee trawl, the 1973-76 cruises a #41 Yankee trawl. Numbers in parentheses are retransformed values.

		I		II		III		IV	
Site group		1968-72	1973-76	1968-72	1973-76	1968-72	1973-76	1968-72	1973-76
No. of stations		237	188	92	90	138	53	110	112
Abundance log (x + 1)	$\bar{x}$	2.19(154)	2.47(296)	2.40(252)	2.62(416)	2.17(149)	2.35(224)	2.16(144)	2.36(230)
	SD	0.40	0.45	0.54	0.40	0.68	0.67	0.54	0.51
Biomass (kg) log (x + 1)	$\bar{x}$	1.70(50)	1.97(95)	1.79(62)	2.14(138)	1.58(38)	1.92(84)	1.56(37)	1.65(45)
	SD	0.40	0.36	0.54	0.43	0.59	0.51	0.57	0.46
No. of species	$\bar{x}$	10.1	12.4	9.7	12.1	8.1	8.8	9.1	13.1
	SD	2.8	3.0	2.9	2.5	2.9	3.3	3.3	4.3
Depth (m)	range	18-101	18-90	24-329	29-152	18-349	27-152	66-379	53-341
	$\bar{x}$	50.0	46.5	117.9	78.9	84.1	75.2	222.1	194.0
	SD	17.3	15.4	46.8	21.9	54.2	33.2	78.3	72.1
Temperature (°C)	range	2-9	3-11	4-14	7-16	5-13	5-14	5-16	5-15
	$\bar{x}$	4.6	6.0	10.0	9.6	8.9	10.2	10.1	11.4
	SD	1.5	1.5	2.1	2.0	2.2	2.1	2.0	1.6

Delaware Bay. This group was generally contained behind a strong thermal gradient and exhibited the warmest bottom temperatures in the study area. These groups were assigned to site group I for the pooled analyses (Fig. 6, Table 2). Extending northward from these groups along the inner shelf was a second, colder site group which tended to be constricted toward shore between northern Long Island and Cape Cod (group II). During 1973 and 1974, when thermal stratification was weaker and inshore water temperatures in the north were higher, there was no distinct break between northern and southern inshore station groups (groups I and II), but instead there were two station groups with members in both northern and southern inshore and mid-shelf waters. One group from each of these years was assignable to each of the two major pooled groups based on faunal similarity; but such assignment, of course, led to the geographical overlap between groups I and II seen off Long Island and Chesapeake Bay in Figure 6.

One or two site groups each year occurred on the northern mid-shelf primarily between 35 and 90 m, in the region of the coolest shelf waters (group

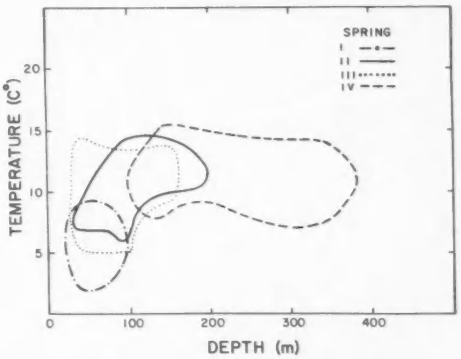


FIGURE 5.—Temperature-depth envelopes for pooled spring site groups, Middle Atlantic Bight area, 1968-76. To avoid distortions introduced by misclassified stations, points falling over two standard deviations from either mean were excluded.

TABLE 2.—Hydrographic and average catch parameters by site group for Fall NMFS Groundfish Survey cruises, Middle Atlantic Bight, 1967-75. All cruises used a #36 Yankee trawl. Numbers in parentheses are retransformed values.

Site group		I	II	III	IV	V
No. of stations		114	176	209	382	114
Abundance log (x + 1)	$\bar{x}$	2.19(130)	2.30(200)	2.20(249)	2.05(111)	1.92(84)
	SD	0.73	0.59	0.57	0.67	0.54
Biomass (kg) log (x + 1)	$\bar{x}$	1.55(36)	1.78(61)	1.73(54)	1.09(11)	0.86(6)
	SD	0.58	0.56	0.59	0.56	0.39
No. of species	$\bar{x}$	8.2	10.8	10.8	6.8	9.3
	SD	3.7	3.6	4.1	2.9	3.7
Depth (m)	range	18-123	20-80	31-192	16-397	71-433
	$\bar{x}$	33.8	42.6	61.5	110.6	249.6
	SD	12.7	12.4	17.1	60.2	77.4
Temperature (°C)	range	8-23	6-25	5-22	6-21	6-18
	$\bar{x}$	16.7	13.4	10.7	11.7	10.4
	SD	3.5	3.5	2.6	2.2	1.9

FIGURE 6.— Pooled site groups based on cluster analysis for fall NMFS Groundfish Survey cruises, 1967-75.

III). The remaining site groups could be classified as outer shelf-shelf break (group IV) or upper slope (group V). The outer shelf-shelf break group displayed a wide depth range and a temperature range very similar to groups II and III, but occurred consistently offshore of those two groups (Fig. 6). The upper slope group had the most restricted temperature range and was bathymetrically discrete from the inner- and mid-shelf groups. The temperature-depth envelopes for the first four site groups (Fig. 7) show a large amount of overlap in the shallower portion of the study area, but much of this overlap is an artifact of combining data across years and over a wide area (i.e., thermal ranges and boundaries between groups varied between years, and bathymetric boundaries varied with latitude).

Species Associations

Between 6 and 11 species clusters were recognized for each cruise (Colvocoresses and Musick 1979). As with the station clusters, although there was some variation in group composition and dis-

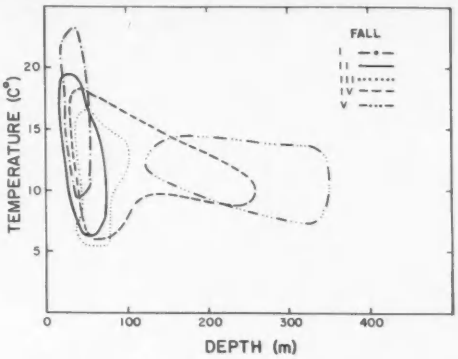
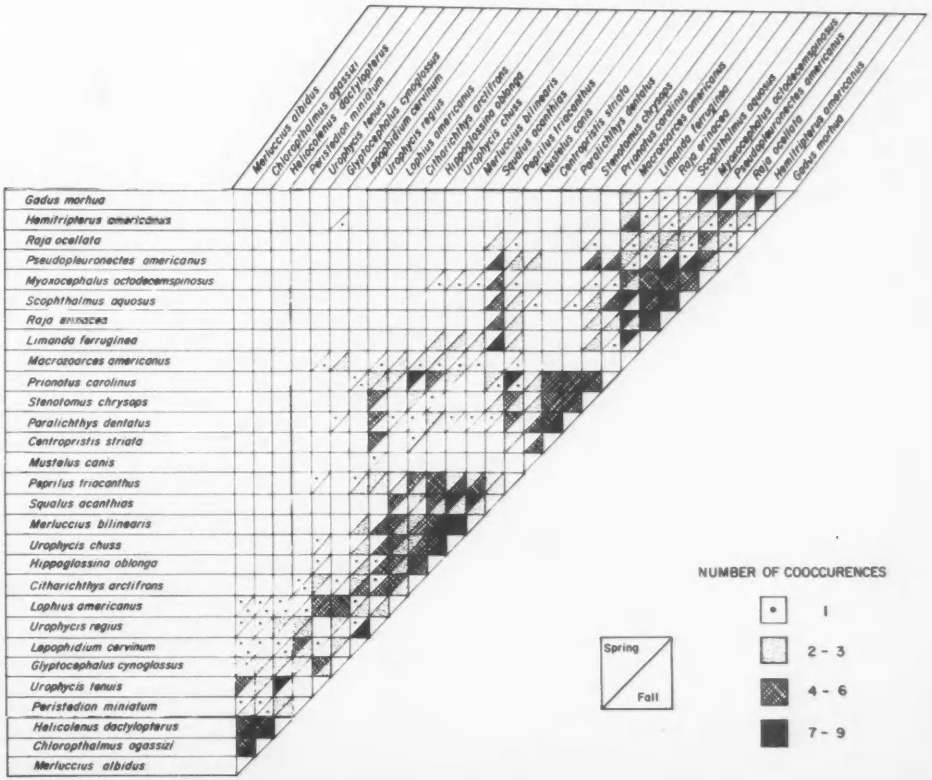


FIGURE 7.—Temperature-depth envelopes for pooled fall site groups, Middle Atlantic Bight area, 1967-75. To avoid distortions introduced by misclassified stations, points falling over two standard deviations from either mean were excluded.

tribution from year to year, the groupings were largely consistent over the 9-yr period of this study. Figure 8 shows the number of times the 30 most commonly occurring and dominant demersal species occurred within the same species group during the spring and fall cruises. The species are arranged so as to be closest to those species they occurred with most often in the clusters, i.e., so that the densest cells fall along the diagonal border of the diagram.

Four strongly recurring species groups are evident from this diagram. *Myoxocephalus octodecemspinosus, Scophthalmus aquosus, Raja erinacea*, and *Limanda ferruginea* frequently appeared in the same group during both seasons. In the spring they were often joined by *Macrozoarces americanus*, a species generally absent from the

FIGURE 8.—Cooccurrences within the same species cluster group for major species, spring and fall NMFS Groundfish Survey cruises, Middle Atlantic Bight area, 1967-76.



clusters in the fall, while *Squalus acanthias* and *Pseudopleuronectes americanus* were common co-group members during the fall cruises. In the spring the latter species regularly occurred in a separate group which included *Gadus morhua* and *Hemitripterus americanus*. Except for *Scophthalmus aquosus*, an inshore resident, all of these species are of boreal faunal affinity and are restricted to cold water (Bigelow and Schroeder 1953; Leim and Scott 1966).

Prionotus carolinus, *Stenotomus chrysops*, *Paralichthys dentatus*, and *Centropristis striata*, all warm-temperate species, were regularly classified in the same group during both seasons. During the fall this group was often joined by *Mustelus canis*, another warm-temperate species which was only rarely taken during the spring cruises. Two other warm-temperate species, *Peprilus triacanthus* and *Urophycis regia*, regularly cooccurred with this group in the spring.

Merluccius bilinearis and *Urophycis chuss* were the two most consistently cooccurring species, appearing in the same group in all but one cruise. These two species formed the core of a third species group which was ubiquitous in the spring and widespread across the deeper portion of the study area in the fall. Both of these boreal species have broader temperature tolerances than the cold-water groups noted above (Musick 1974; Bigelow and Schroeder 1953). Abundances of these two species were greater on the outer shelf and shelf break, and they often clustered with *Paralichthys oblongus* (= *Hippoglossina oblonga*), an outer shelf resident, and, in the fall, with *Citharichthys arctifrons*, a slope resident which also occurs on the outer shelf (Richardson and Joseph 1973) and *Lepophidium cervinum*, another outer shelf resident. The warm-temperate species *Peprilus triacanthus* and *Urophycis regia* were also common group members in the fall, while *Lophius americanus* regularly occurred in this group in the spring.

The fourth clearly defined recurring species group was an upper slope group composed of *Helicolenus dactylopterus*, *Chloropthalmus agassizi*, and *Merluccius albidus*, which appeared consistently during both seasons. *Urophycis tenuis* commonly cooccurred with members of this group during the spring, while in the fall this species was more widely distributed across the outer shelf and tended to appear in small groups with *Lophius americanus* and *Glyptocephalus cynoglossus*.

The major recurring species groups described above are listed for each season in Table 3. The groups are ordered in the same manner as the generalized station groups, that is, from shallowest to deepest (distribution) while still maintaining nearest neighbor intergroup relationships as determined in the clusters. Figures 9 and 10 show the distributional relationships between the major site and species groups as determined by nodal analyses. As noted above, these relationships are more sharply defined during the spring cruises than in the fall, but in both cases the nodal analyses show clear differences in the faunal composition of site groups and the distribution of species groups. The interrelationships seen here are also highly representative of those noted during analyses of the individual cruises.

Dominance

The dominant species for each of the pooled site groups are given in Tables 4 and 5. During the spring *Limanda ferruginea* was the major dominant at the cold-water, inshore site group (I), *Squalus acanthias* and *Merluccius bilinearis* were among the major dominants at all site groups, and *Peprilus triacanthus* was a major dominant at all but the cold-water site group. *Stenotomus chrysops* was a major dominant along the southern outer shelf (group III). In the fall, the southern inshore site group (I) was strongly dominated by three warm-temperate species: *Prionotus carolinus*, *Stenotomus chrysops*, and *Peprilus triacanthus*. These three species persisted as major dominants at the northern inshore site group, but were joined there in roughly equal dominance by three boreal species: *Limanda ferruginea*, *Squalus acanthias*, and *Merluccius bilinearis*. *Peprilus triacanthus* and the latter group were major dominants on the northern mid-shelf (group III). *Peprilus triacanthus* and *Merluccius bilinearis* were also major dominants at the outer shelf stations (group IV), where they were joined by *Urophycis regia*. The shelf-break stations (group V) were dominated by *Merluccius bilinearis*, *Citharichthys arctifrons*, and *Helicolenus dactylopterus*.

There were few major changes in species dominance throughout the study, and Tables 4 and 5 are representative of those for the individual cruises. *Merluccius bilinearis*, *Peprilus triacanthus*, and *Squalus acanthias* were consistently the three most dominant species during both major seasons. Although *Merluccius bilinearis* accounted for only around 10% of the individuals taken, it was the most consistently dominant

TABLE 3.—Major recurrent species groups, NMFS Groundfish Survey, Mid-Atlantic Bight area, 1967-76. Faunal affinity is designated after each species name: Boreal, Bo; warm temperate, WT; inner shelf resident, IS; outer shelf resident, OS; slope resident, SI.

Spring cruises	Fall cruises
A	A
Gadus morhua Bo	*Centropristes striata* WT
Hemitripterus americanus Bo	*Mustelus canis* WT
Pseudopleuronectes americanus Bo	*Paralichthys dentatus* WT
	Prionotus carolinus WT
B	*Stenotomus chrysops* WT
Limanda ferruginea Bo	B
Macrozoarces americanus Bo	
Myoxocephalus octodecemspinosus Bo	*Limanda ferruginea* Bo
Raja erinacea Bo	*Myoxocephalus octodecemspinosus* Bo
Scopthalmus aquosus IS	*Pseudopleuronectes americanus* Bo
	Raja erinacea Bo
C	*Scophthalmus aquosus* IS
Lophius americanus Bo	*Squalus acanthias* Bo
Merluccius bilinearis Bo	C
Paralichthys oblongus OS	
Squalus acanthias Bo	*Citharichthys arctifrons* OS
Urophycis chuss Bo	*Lepophidium cervinum* OS
	Merluccius bilinearis Bo
D	*Paralichthys oblongus* OS
	Peprilus triacanthus WT
Centropristes striata WT	*Urophycis chuss* Bo
Paralichthys dentatus WT	*Urophycis regia* WT
Peprilus triacanthus WT	
Prionotus carolinus WT	D
Stenotomus chrysops WT	
Urophycis regia WT	*Glyptocephalus cynoglossus* Bo-SI
	Lophius americanus Bo
E	*Urophycis tenuis* Bo-SI
Chloropthalmus agassizi SI	E
Helicolenus dactylopterus SI	
Merluccius albidus SI	*Chloropthalmus agassizi* SI
Urophycis tenuis Bo-SI	*Helicolenus dactylopterus* SI
	Merluccius albidus SI

species, reflecting a very uniform distribution. *Limanda ferruginea* was the only major species to undergo a notable change in dominance, showing a pronounced decline only during the last 2 yr of the study. Parrack[4] has carefully linked the decline of this valuable commercial species to overfishing.

Squalus acanthias and *Peprilus triacanthus*, two of the most dominant species, showed strong seasonal differences in the groups with which they clustered. *Squalus*, a boreal cold-water species, was widespread in the spring and occurred in the ubiquitous group, but during the fall cruises this species was restricted to the cooler waters on the northern shelf and generally clustered with the *Limanda*-dominated cold-water group. *Peprilus triacanthus* generally appeared in the same group as the other warm-temperate species in the spring when it was distributed along the outer shelf, but in the fall this species was widespread across the shelf and tended to be more concentrated in the cooler portions of the study area and usually clustered with the semi-ubiquitous *Merluccius bilinearis-Urophycis chuss* group. *Peprilus triacanthus* is considerably more tolerant of cooler temperatures than the other warm-temperate species encountered in this study (Horn 1970). *Urophycis regia*, another warm-temperate species which inhabits cooler waters (Struhsaker 1969), clustered similarly to *Peprilus triacanthus*, occurring with the warm-temperate group in the spring and with the semi-ubiquitous group in the fall; however, it appeared to have slightly narrower temperature tolerances, as it was more restricted to the southern portion of the outer shelf in spring and tended to be more concentrated in deeper, warmer waters in the fall.

Absolute abundances, both of total catches and of individual species, varied to a much greater extent than did the relative abundances between species throughout the study. Because abundance trends for the fall cruises have been well documented by Clark and Brown (1977) and the change

[4]Parrack, M. L. 1973. Current status of the yellowtail flounder fishery in ICNAF Subarea 5. Int. Comm. Northw. Atl. Fish., Res. Doc. 73/104, Ser. No. 3067, 3 p.

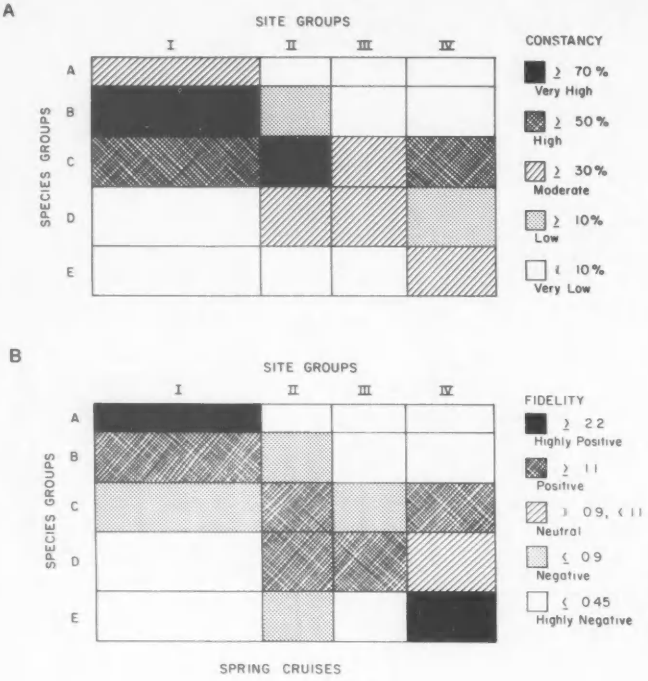


FIGURE 9.—Nodal constancy (A) and fidelity (B) diagrams showing the interrelation between pooled site and species groups, NMFS Groundfish Survey spring cruises, 1968-76.

TABLE 4.—Dominant species by site group for Spring NMFS Groundfish Survey cruises, Mid-Atlantic Bight area, 1968-76. A species was considered dominant if it occurred among the five most abundant species at at least 20% of all stations in the site group. Figures given are percentage of stations within each site group at which a species occurred (%) and the average percentage that the species contributed towards total abundance of nonpelagic fishes ($\bar{x}$%) within the site group. Faunal affinities and species groups are as given in Table 3.

Species	Faunal affinity	Species group	Site group I		II		III		IV	
			%	$\bar{x}$%	%	$\bar{x}$%	%	$\bar{x}$%	%	$\bar{x}$%
Gadus morhua	Bo	A	44	1.4						
Pseudopleuronectes americanus	Bo	A	38	2.2						
Limanda Ferruginea	Bo	B	88	28.5	22	1.4				
Macrozoarces americanus	Bo	B	68	5.2						
Myoxocephalus octodecemspinosus	Bo	B	56	5.0						
Raja erinacea	Bo	B	77	11.9	52	1.5				
Scophthalmus aquosus	IS	B	70	4.7						
Hippoglossina oblonga	OS	C	29	1.1	84	7.6	44	2.4	63	5.2
Lophius americanus	Bo	C			58	0.7			53	1.4
Merluccius bilinearis	Bo	C	79	20.5	97	22.4	66	13.0	90	27.2
Squalus acanthias	Bo	C	73	11.1	87	30.0	82	24.6	58	12.2
Urophycis chuss	Bo	C	54	3.9	84	9.3	25	1.9	74	9.5
Centropristes striata	WT	D					40	4.2		
Paralichthys dentatus	WT	D					47	2.2		
Peprilus triacanthus	WT	D			75	14.8	57	12.3	56	19.4
Prionotus carolinus	WT	D			50	7.1	51	9.8		
Stenotomus chrysops	WT	D			24	2.1	50	15.6		
Urophycis regius	WT	D					48	7.2	35	2.0
Chloropthalmus agassizi	SI	E							31	1.6
Helicolenus dactylopterus	SI	E							59	6.7
Merluccius albidus	SL	E							38	3.1
Urophycis tenuis	Bo-SI	E							38	1.6

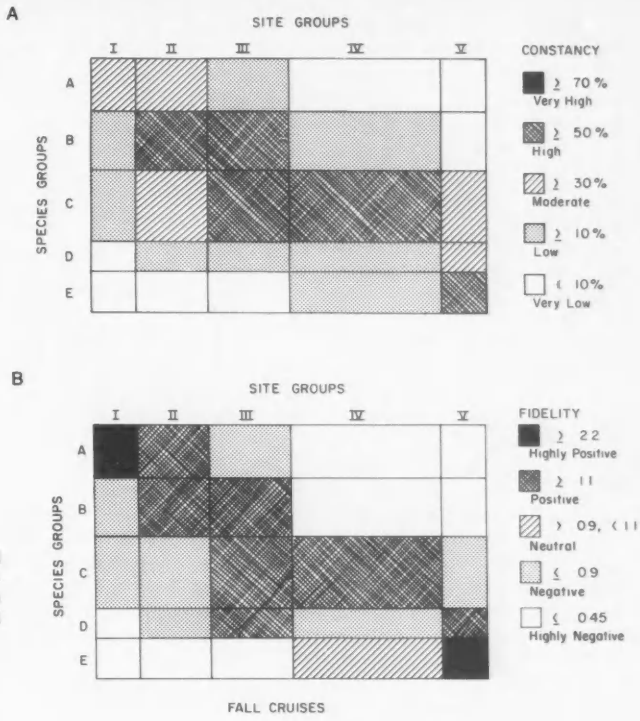


FIGURE 10.—Nodal constancy (A) and fidelity (B) diagrams showing the interrelation between pooled site and species groups, NMFS Groundfish Survey fall cruises, 1967-75.

TABLE 5.—Dominant species by site group for Fall NMFS Groundfish Survey cruises, Mid-Atlantic Bight area, 1967-75. A species was considered dominant if it occurred among the five most abundant species at at least 20% of all stations in the site group. Figures given are percentage of stations within each site group at which a species occurred (%) and the average percentage that the species contributed towards total abundance of nonpelagic fishes ($\bar{x}$%) within the site group. Faunal affinities and species groups are as given in Table 3.

Species	Faunal affinity	Species group	Site group I		II		III		IV		V	
			%	$\bar{x}$%	%	$\bar{x}$%	%	$\bar{x}$%	%	$\bar{x}$%	%	$\bar{x}$%
Centropristes striata	WT	A	50	4.7								
Mustelus canis	WT	A	38	5.7								
Paralichthys dentatus	WT	A	61	6.7	51	13.5						
Prionotus carolinus	WT	A	75	33.3	61	10.1						
Stenotomus chrysops	WT	A	53	17.5	51	13.5	30	2.4				
Limanda ferruginea	Bo	B			65	14.1	79	18.0				
Myoxocephalus octodecemspinosus	Bo	B					52	2.7				
Pseudopleuronectes americanus	Bo	B			69	3.3	47	1.7				
Raja erinacea	Bo	B			64	3.8	58	2.7				
Scophthalmus aquosus	IS	B	52	2.9	62	3.4	25	1.0				
Squalus acanthias	Bo	B			69	16.8	77	11.3	23	5.1		
Citharichthys arctifrons	OS	C					35	2.7	49	6.4	68	11.8
Hippoglossina oblonga	OS	C			59	2.2	70	3.3	53	3.6	34	1.4
Lepophidium cervinum	OS	C							32	2.9	27	2.9
Merluccius bilinearis	Bo	C			67	10.2	92	23.0	80	20.8	58	11.3
Peprilus triacanthus	WT	C	59	15.8	65	11.1	72	19.6	65	26.5	28	5.1
Urophycis chuss	Bo	C			35	2.7	74	8.2	37	4.2	30	2.1
Urophycis regius	WT	C	40	6.5					57	14.8	40	7.9
Lophius americanus	Bo	D							31	2.2	57	3.0
Chloropthalmus agassizi	SI	E									44	5.9
Helicolenus dactylopterus	SI	E									84	21.2
Merluccius albidus	SI	E									65	7.7

in nets makes a similar analysis of the spring cruises tenuous at best, we will not consider the topic further other than to note that average abundance and biomass were higher in the northern and inshore portion of the study area during both seasons (Tables 1, 2).

CONCLUSIONS

Despite large variation in the abundances of individual species, cluster analyses of 9 yr of survey data have shown clear and consistent patterns of community composition and distribution among demersal fishes of the Middle Atlantic continental shelf. Allowing for thermal variation and misclassification of small catches, persistent site and species clusters have indicated the presence of four relatively constant and well-defined areas of faunal homogeneity in the spring and five more general areas in the fall, and five strongly recurring species associations during both seasons.

The spring site groups can be described approximately as northern inner- and mid-shelf (I), extending from shore out to about 60-80 m from Cape Cod to south of Delaware Bay; northern mid-shelf (II), occupying from around 60-80 m out to about 150 m from Cape Cod to Hudson Canyon; southern outer shelf (III), 60-150 m, from Delaware Bay to Cape Hatteras; and outer shelf-shelf break (IV), >150 m. The southern inner and mid-shelf is a thermally related transition zone between groups I and III. The outer shelf between Delaware Bay and Hudson Canyon was also a transition zone (between groups II and III), but this discontinuity does not appear to be related directly to temperature, but rather to the extent to which the northward migration of the warm-temperate species group has progressed by the time of the survey.

The five spring species groups contained one group specific to this season and four which contained common elements and properties with analogous fall groups. The first group (A) can be characterized as highly cryophilic, being virtually restricted to site group I and containing two members (*Gadus morhua* and *Hemitripterus americanus*) which were relatively absent from the study area during the fall. None of these species were major dominants, even within group I. The second group (B) is also composed of primarily boreal, cold-water species, but in this case is not completely restricted to site group I (although primarily distributed there) and contains the major dominant for that site, *Limanda ferruginea*. The third group (C) may be described as ubiquitous throughout the study area with moderate or better constancy to all site groups (Fig. 9). All members of this group are boreal or resident, and the major dominants, *Merluccius bilinearis* and *Squalus acanthias*, are the nuclear members. The fourth group (D) is composed entirely of warm-temperate members and is restricted to the warmer southern and outer shelf waters (site groups II-IV). *Peprilus triacanthus* and *Stenotomus chrysops* are the major dominants from this group. The last group (E) is composed strictly of weakly dominant slope species mostly confined to the shelf break site group (IV).

The spring warming trend noted during the study period appeared to have no major effect on the composition and distribution of fish communities in the area other than the latitudinal division between the inshore site groupings. The results of the present study are very much in accordance with the conclusions of Taylor et al. (1957) and Colton (1972) who found that while the ranges and distributions of certain species did shift with a changing thermal regime, there were no obvious overall changes in faunal composition. This is understandable when one considers that the average change encountered (about 2°C) is relatively small compared with the temperature tolerances of the species involved and the seasonal and geographic temperature variation encountered.

The five fall site groups can best be described as southern inner- and mid-shelf (I), extending out to about 60 m from Cape Hatteras to Delaware Bay and containing the area of warmest temperatures; northern inner shelf (II), extending northward from group I along a similar depth regime and containing cooler waters; northern mid-shelf (III), extending from group II out to about 90 m and occupying the area of the cold pool; outer shelf (IV), occupying the area between groups I and III and about 150 m; and shelf break (V), >150 m. While, again, with these groups there is some overlap (particularly with groups I and II as discussed above), their definition is fairly good considering the rapidly changing environmental conditions and migratory activity of fish during this period.

The fall species associations, as noted above, have much in common with those noted in the spring. The small cryophilic group is absent, but the terms applied to the other four spring groups may be applied here as well. An exclusively boreal-resident group (B) persists on the northern inner- and mid-shelf, including four members of

the spring cold-water group B, one member of the cryophilic group, and *Squalus acanthias*, a ubiquitous dominant in the spring found only in the northern portion of the study area in the fall. The ubiquitous spring group (C) persists with *Merluccius bilinearis* the major dominant, and two other common members from the spring group, but the fall group is no longer exclusively boreal-resident in faunal affinity and the group is distributed primarily in more northerly and deeper waters. Two warm-temperate species, *Peprilus triacanthus* and *Urophycis regia*, join this group as major dominants, while the other warm-temperate species, dominated by *Prionotus carolinus* and *Stenotomus chrysops*, continue to occur in the same group (A) but show a dramatic change in distribution, occurring on the inner shelf rather than the outer as in the spring. The shelf break group (E) shows the same composition and distribution as in the spring, while the fifth group (D), which did not occur in the spring, is composed of nondominant eurybathyic species which occur sporadically across all but the southern inner site group.

It is obvious that although the two sampling periods included the two extremes of average water temperatures in the study area, the fall (warm extreme) is a much more dynamic period than the spring (cool extreme) for the fish communities in the region. This appears to be related in large part to the much less stable thermal regime encountered in the fall, particularly in shallower portions of the study area. Thermal gradients developed during the warmer months on the inner shelf are much stronger than those encountered on the mid-shelf during the spring, and because cooling waters mix or turn over while warming waters stratify, the fall gradients break down much more quickly than those in the spring. As a result, a fish community in this region may be subjected to rapidly changing environmental temperatures by a number of factors. A relatively small shift of water masses in the vicinity of a strong thermal gradient, migration across a gradient, or rapid cooling and mixing along the gradient all subject these communities to abrupt changes of temperature (Parr 1933), and it is not surprising that the site groupings based on faunal similarities found in the inner portion of the study area during the fall exhibited wide temperature ranges (Fig. 7). Parr (1933) pointed out that the temperature-related distributions of organisms in the vicinity of a strong thermal gradient may be more influenced by the magnitude of short-term temperature changes than by the actual temperatures encountered. This concept may well have application to the formation of the three innermost site groups identified during the fall; for although the groups strongly overlap with respect to the temperature ranges encountered, there is a considerable difference in the strength of the thermal gradients and presumably the short-term temperature variations encountered within each, with group I being primarily sited in the region of the sharpest gradients and group III being located in the most thermally stable area.

The distributional patterns noted in this paper lead to the conclusion that continental shelf demersal fish communities in the Middle Atlantic Bight are largely structured by temperature on the inner- and mid-shelf and by depth on the outer shelf and shelf break. This is not at all unexpected considering the sedimentary and topographical uniformity of the inner- and mid-shelf (Emery and Uchupi 1972) and the large annual variation in bottom-water temperature in the inshore region, with the converse holding true along the outer shelf and shelf break. Scott (1982) found the distributions of a number of groundfish species on the Scotian Shelf to be related to bottom sediment type. Although substrate preference indices were not generated during the present study, comparisons of species group distribution with bottom sediment type maps do not indicate any strong species group-sedimentary relationships. This contrast may be the result of two major differences between the continental shelves in the Middle Atlantic Bight and off Nova Scotia; there is a much more variable sedimentary environment and a considerably smaller annual range of bottom-water temperatures on the Scotian Shelf.

Tyler (1971) examined latitudinal variation in the regular and seasonal components of several nearshore Atlantic marine fish communities, and concluded that the proportion of seasonal and occasional components to regular components varied directly with annual variation in water temperature. The results of the present study are certainly in accord with this conclusion, in that the most highly variable area in terms of annual water temperature variation (the southern inner- and mid-shelf) was also the most variable area in terms of community composition, but it is also evident that Tyler's statement cannot be taken axiomatically. The outer shelf, although very homothermic, was also subject to considerable seasonal variation in community structure because of the changing relationship between the

stable thermal regime on the outer shelf and the highly varying regime in adjacent inshore waters. During the spring, when inshore water temperatures were depressed well below those on the outer shelf, the outer shelf served as a refuge for the warm-temperate species association which occurs largely inshore when water temperatures there become elevated above those on the outer shelf.

It is also interesting to note that while for the most part the communities observed here are structured by species associations that behave as a group in response to environmental variation, two of the most successful species (*Peprilus triacanthus* and *Squalus acanthias*) are those which show the least permanent group affinities. As noted above, the success of *P. triacanthus* may be due in part to the species' very wide thermal tolerance, but *S. acanthias* was one of the more thermally restricted species encountered in the study, being restricted to waters less than 14°C.

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EARLY ZOEAL STAGES OF *PLACETRON WOSNESSENSKII* AND *RHINOLITHODES WOSNESSENSKII* (DECAPODA, ANOMURA, LITHODIDAE) AND REVIEW OF LITHODID LARVAE OF THE NORTHERN NORTH PACIFIC OCEAN

EVAN B. HAYNES[1]

ABSTRACT

Stage I zoeae of *Placetron wosnessenskii*, and Stage I and Stage II zoeae of *Rhinolithodes wosnessenskii*, which were reared in the laboratory, can be distinguished from other described zoeae of Lithodidae: *P. wosnessenskii* have long, blunt spines on posterior margins of abdominal somites 2-5 and sinuate curvature of long, blunt, posterolateral spines on abdominal somite 5; *R. wosnessenskii* zoeae have a spine in the middorsal, posterior portion of the carapace. Zoeae of Lithodidae can be distinguished from zoeae of Pagurinae by body shape, size of the eyes, spines on the carapace, development of uropods, and presence or absence of the anal spine. Stages of lithodid zoeae can be distinguished by eye attachment, number of natatory setae on maxillipeds, and development of pleopods, uropods, and telson. Keys, based on spination of the carapace, rostrum, abdomen, and telson, distinguish between zoeae and glaucothoe of each described species of Lithodidae from the northern North Pacific Ocean.

Crabs of the family Lithodidae constitute a major component of the reptant decapod fauna of the northern North Pacific Ocean. Of about 25 species of Lithodidae in the northern North Pacific Ocean, larvae have been described, at least in part, for eight species: *Dermaturus mandtii* Brandt, *Cryptolithodes typicus* Brandt, *Hapalogaster grebnitzkii* Schalfeew, *H. mertensii* Brandt, *Lithodes aequispina* Benedict, *Paralithodes brevipes* (Milne Edwards and Lucas), *P. camtschatica* (Tilesius), and *P. platypus* Brandt. Most descriptions are scattered in foreign scientific journals, however, and published reviews of the larvae are limited in species and scope. This report describes and illustrates Stage I zoeae of *Placetron wosnessenskii* Schalfeew and Stages I and II zoeae of *Rhinolithodes wosnessenskii* Brandt reared in the laboratory from ovigerous females. I characterize the morphological differences between zoeae of the Lithodidae and subfamily Pagurinae (family Paguridae), compare the morphology of lithodid larvae of the northern North Pacific Ocean, and provide keys for identifying the described larvae to species and stage.

METHODS AND RESULTS

In March 1982, ovigerous females of *Placetron wosnessenskii* and *Rhinolithodes wosnessenskii* were collected near Auke Bay, Alaska, in traps and by divers using scuba. The females were transported to the laboratory and kept in filtered seawater (about 6°C) until the zoeae hatched about 1 wk later. After hatching, about 50 zoeae of each species were transferred to each of four 4 l glass jars containing about 2,500 ml of seawater at 6.1°C. Seawater in the jars was changed about every other day. Zoeae were fed live plankton strained through a 0.333 mm mesh. About 10 ml of live plankton was added to each jar every other day. The live plankton consisted mostly of phytoplankton and barnacle nauplii. A more detailed description of the rearing system and type and duration of illumination is given in Haynes and Ignell (1983).

Zoeae of *Placetron wosnessenskii* hatched at night, and samples of zoeae were taken the following morning. No prezoeae of *P. wosnessenskii* were seen. *Rhinolithodes wosnessenskii* zoeae hatched at night and during the day, and those examined about 10 min after hatching had remnants of prezoeal exuviae attached to the cephalothorax and telson. The remnant exuviae are not described in this paper.

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Although food was seen in the guts of some *Placetron wosnessenskii* zoeae, none molted to Stage II. Zoeae of *Rhinolithodes wosnessenskii* fed actively and molted to Stage II about 20 d after hatching. Failure to change the seawater on schedule prevented rearing the zoeae of *R. wosnessenskii* beyond Stage II.

DESCRIPTION OF ZOEAE

Terminology, methods of measuring zoeae and their appendages, techniques of illustration, and nomenclature of appendages follow Haynes (1979). Carapace length refers to the straight-line distance from posterior margin of eye orbit to middorsal posterior margin of carapace, excluding the middorsal spine. Spines on the telson are numbered from the outermost to innermost (medial) pair. Setation formulae are the number of setae per segment from the distal segment to the proximal segment. For clarity in the illustrations, setules on plumose setae are usually omitted, but

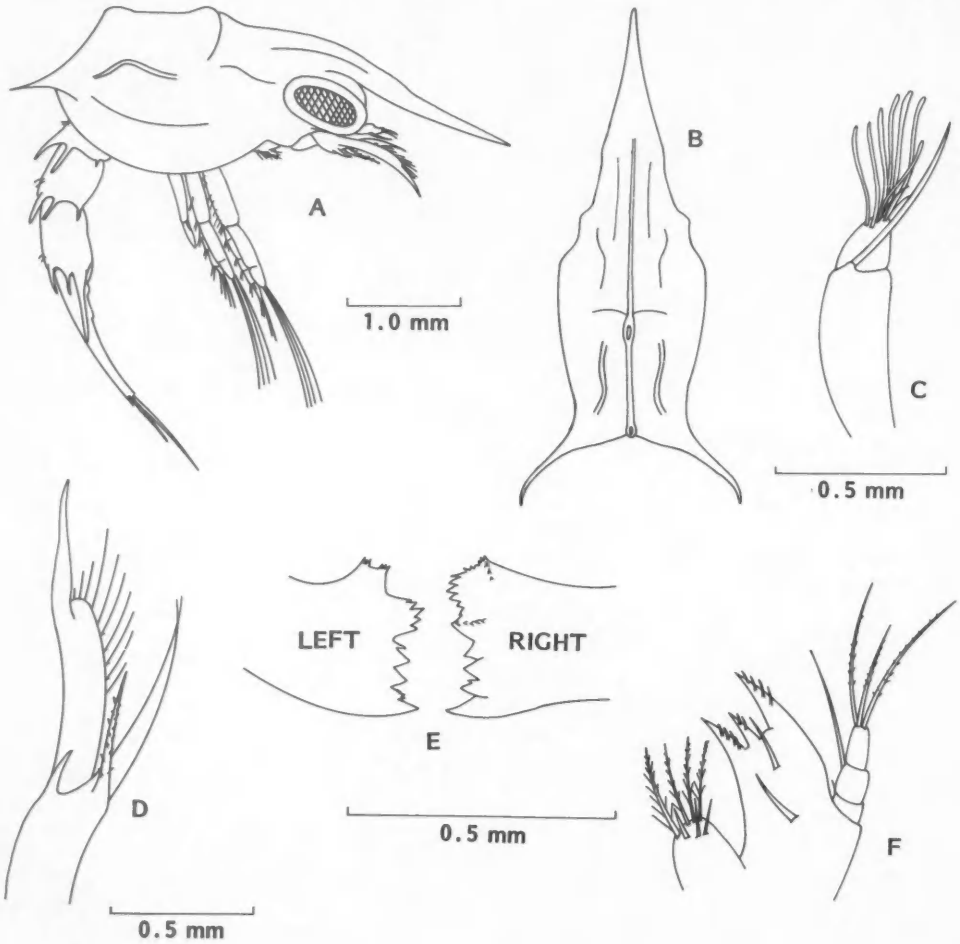
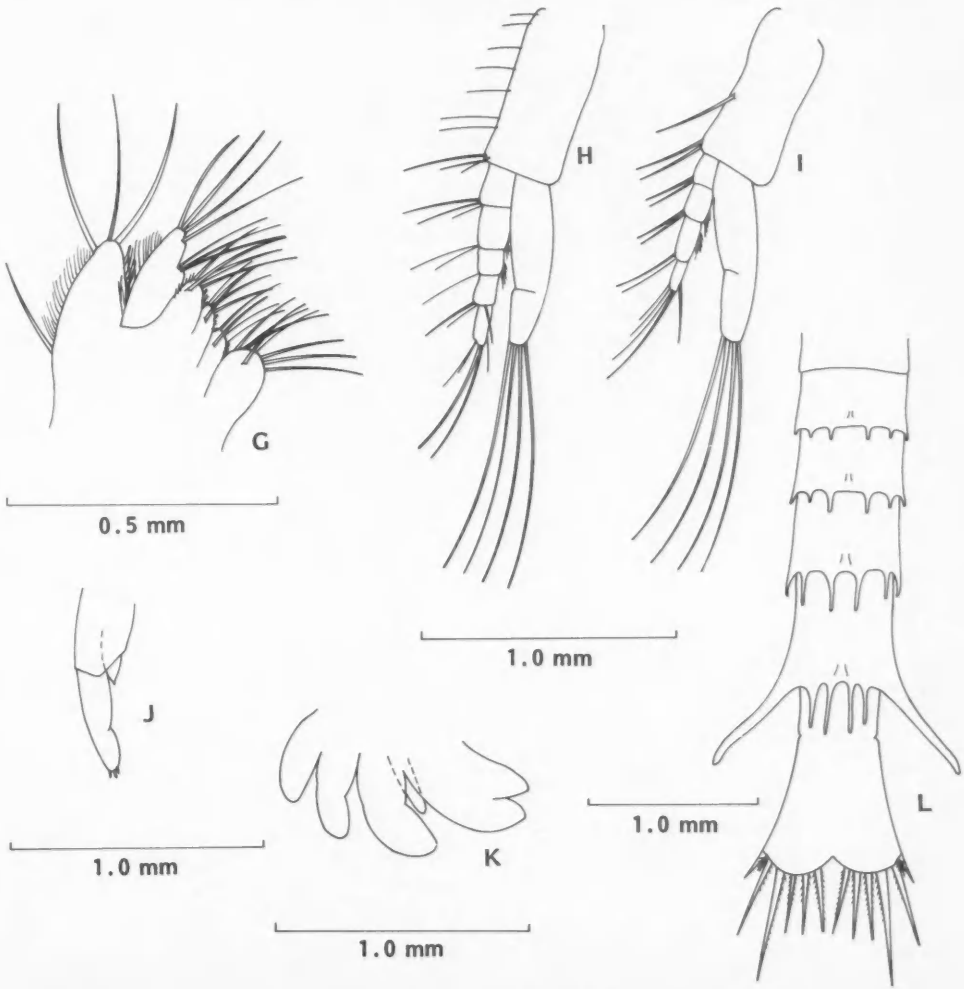


FIGURE 1.—Stage I zoea of *Placetron wosnessenskii*: A, whole animal, right side; B, carapace, dorsal; C, antennule, ventral; D, antenna, ventral; E, mandibles (left and right), posterior; F, maxillule, ventral; G, maxilla, dorsal; H, first maxilliped, lateral;

spinulose setae are shown. Five zoeae were used to verify segmentation and setation; 10 zoeae were used for measurements. Only those morphological characteristics useful for readily identifying each stage are given.

Placetron wosnessenskii — Stage I Zoeae

Mean carapace length, 2.12 mm (range 2.08-2.21 mm, 10 specimens); mean total length, 6.22 mm (range 5.90-6.70 mm, 10 specimens) (Fig. 1A, B). Live zoeae orange throughout except for colorless appendages and posterolateral spines on carapace and abdomen. Carapace with medially curved, long (>1/4 carapace length), posterolateral spines; markedly pronounced lateral ridges and dorsoventral ridge; and two middorsal angular prominences: one near center of carapace and other at posterior edge. No supraorbital spines. Eyes sessile.



I, second maxilliped, lateral; J, third maxilliped, lateral; K, pereopods 1-5, lateral; L, abdomen and telson, dorsal.

Antennule (Fig. 1C).—First antenna (antennule) with unsegmented tubular basal portion (peduncle) and distal conical projection. Peduncle with ventral plumose seta. Conical projection with seven aesthetascs and two simple setae terminally.

Antenna (Fig. 1D).—Second antenna (antenna) with inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, shorter than scale, and tipped with two simple setae. Antennal scale without distal joint, has fringe of 10 heavily plumose setae along terminal inner margin and prominent spine on distal outer margin. Ventral surface of protopodite with spinulose spine at base of flagellum and naked spine at base of antennal scale.

Mandible (Fig. 1E).—Incisor process of right mandible a tooth; left mandible with biserrate incisor process. Anterior margins of each mandible with premolar denticles. Mandibles without subterminal processes or movable premolar denticle (lacinia mobilis).

Maxillule (Fig. 1F).—First maxilla (maxillule) with coxopodite, basipodite, and endopodite. Coxopodite (proximal lobe) unsegmented with four large spinulose spines and three simple spines terminally. Basipodite (median lobe) with three spines terminally (each spine with several spinules) and two simple spines subterminally. Three-segmented endopodite originates from lateral margin of basipodite. Endopodite with three setae terminally, a long distal seta on second segment, and a short distal seta on first segment. Fine hairs on inner and outer margins of exopodite, outer margin of endopodite, both lobes of basipodite, and distal lobe of coxopodite.

Maxilla (Fig. 1G).—Second maxilla (maxilla) with platelike exopodite (scaphognathite). Exopodite with three long plumose setae terminally and a subterminal plumose seta on outer margin; no proximal expansion of exopodite. Endopodite unsegmented, setation formula 3, 1, 3. Basipodite and coxopodite bilobed. Basipodite with four setae on distal lobe and five setae on proximal lobe. Coxopodite with four setae on distal lobe and eight (sometimes seven) setae on proximal lobe. Fine hairs on inner and outer margins of scaphognathite, outer margins of endopodite, and distal margins of basipodite and coxopodite.

First maxilliped (Fig. 1H).—Exopodite partially segmented with four natatory setae. Endopodite slightly longer than exopodite and distinctly five segmented; setation formula 5, 3, 1, 2, 3. Protopodite unsegmented with 10 setae.

Second maxilliped (Fig. 1I).—Similar to first maxilliped except endopodite slightly shorter than exopodite. Endopodite four segmented, setation formula 5, 2, 2, 2. Protopodite with three lateral setae.

Third maxilliped (Fig. 1J).—Exopodite and endopodite undeveloped. Exopodite partially segmented, with three undeveloped setae terminally. Endopodite with undeveloped seta terminally.

Pereopods (Fig. 1K).—Poorly developed, without exopodites. First pereopod bilobed. Fifth pereopod arises medially between first and second pereopods.

Abdomen and telson (Fig. 1A, L).—Abdomen with five somites and telson (somite 6 fused with telson). Somites 2-5 have six bluntly tipped spines on posterior margin and two minute dorsal setae. Outer pair of posterior spines on somite 5 are long (about 1.2 times somite width), blunt, and somewhat sinuate. Telson with medial invagination posteriorly and 6 + 6 spines. Third pair of telsonic spines longest (about 3/4 maximum telson width). All spines jointed with telson. Minute seta between spinal pairs 1 and 2 originates from ventral surface; seta often without setules; spinules on spinal pairs 2-6. No uropods or anal spine.

Rhinolithodes wosnessenskii

Stage I Zoeae

Mean carapace length, 1.29 mm (range 1.21-1.34 mm, 10 specimens); mean total length, 4.45 mm (range 4.02-4.62 mm, 10 specimens) (Fig. 2A, B). Cephalothorax and base of maxillipeds orange; remainder of maxillipeds, most of rostrum, and all of abdomen colorless. Carapace with middorsal angular prominence and spine at middorsal posterior margin; medially curving, long (>1/4 carapace length), posterolateral spines; markedly pronounced lateral ridge. No supraorbital or anal spine. Eyes sessile.

Antennule (Fig. 2C).—Distal conical projection unsegmented from peduncle. Peduncle with ventral plumose seta. Conical projection with seven

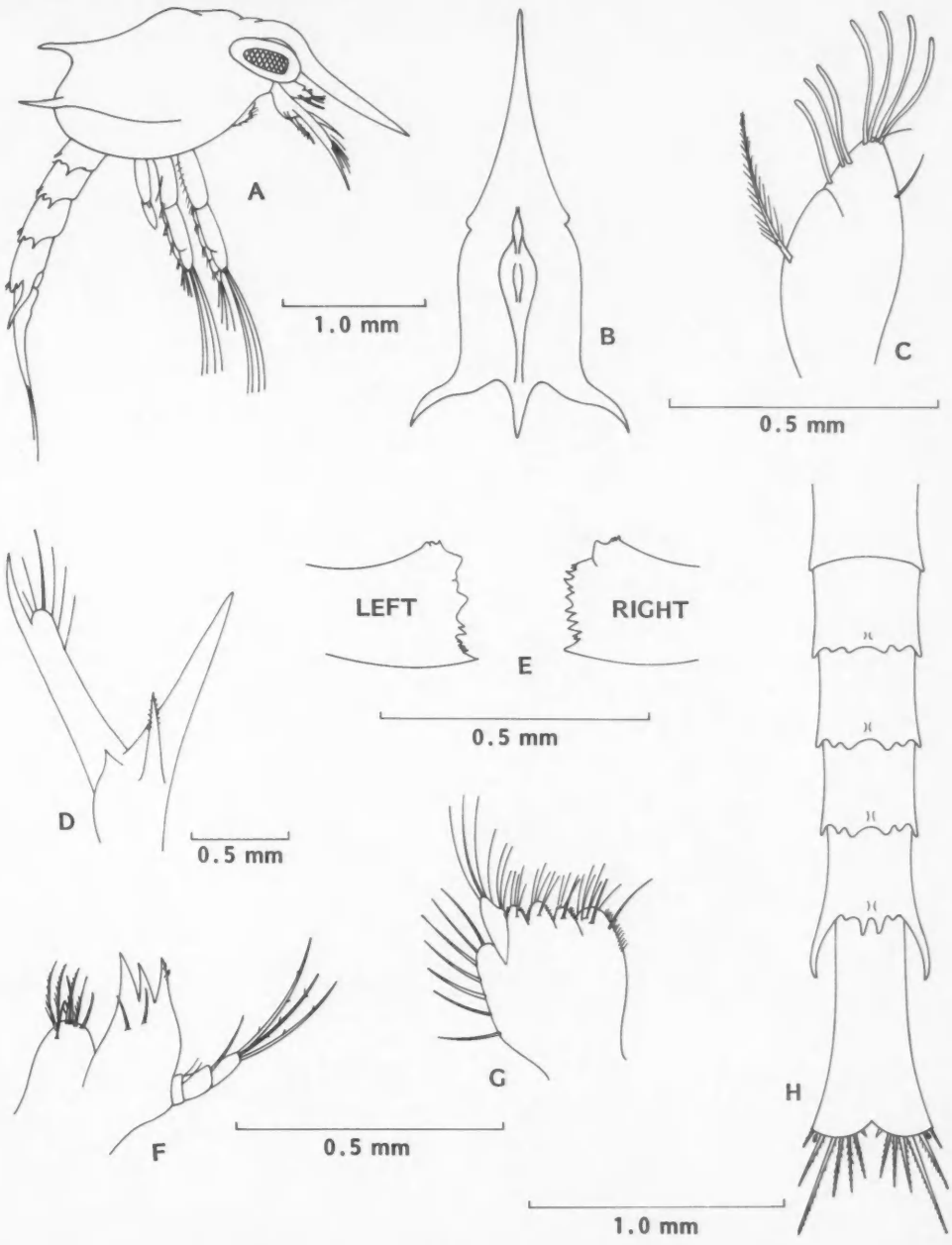


FIGURE 2.—Stage I zoea of *Rhinolithodes wosnessenskii*: A, whole animal, right side; B, carapace, dorsal; C, antennule, ventral; D, antenna, ventral; E, mandibles (left and right), posterior; F, maxillule, ventral; G, maxilla, dorsal; H, abdomen and telson, dorsal.

aesthetascs and two simple setae (one terminal and one lateral).

Antenna (Fig. 2D).—Antenna with inner flagellum and outer antennal scale; flagellum without setae and shorter than scale. Antennal scale unjointed distally, fringed with six heavily plumose setae along terminal and inner margins, and prominent spine distally on outer margin. Ventral surface of protopodite with spinulose spine at base of flagellum and smaller naked spine at base of scale.

Mandible (Fig. 2E).—Incisor processes of left and right mandibles a single tooth. Anterior margins of each mandible with premolar denticles. No subterminal processes or movable premolar denticles.

Maxillule (Fig. 2F).—Similar to Stage I *Placetron wosnessenskii* except spines of basipodite less spinulose and proximal segment of endopodite with two simple setae terminally instead of one.

Maxilla (Fig. 2G).—Scaphognathite with seven long plumose setae on outer margin, no proximal expansion, setation formulae of endopodite, basipodite, and coxopodite same as in Stage I *Placetron wosnessenskii*. Fine hairs on margins of basipodite and coxopodite.

Maxillipeds 1-3 and pereopods 1-5.—Nearly identical in shape and number of setae to those of Stage I *Placetron wosnessenskii*.

Pleopods.—Absent.

Abdomen and telson (Fig. 2A, H).—Short blunt spines on abdominal somites 2-5; length of outer pair on somite 5 about 0.8 times maximum width of somite. Telson with medial invagination and 7 + 7 posterior spines. Third pair of telsonic spines longest, about 3/4 maximum telson width; minute seta between spinal pairs 1 and 2 sometimes without setules; spinules on spinal pairs 2-6. No uropods or anal spine.

Stage II Zoeae

Mean carapace length, 1.30 mm (range 1.21-1.34 mm, 10 specimens); mean total length, 4.81 mm (range 4.02-5.03 mm, 10 specimens). No supraorbital spine. Eyes stalked. Characters not mentioned are nearly identical to characters of Stage I.

Antennule.—Distal conical projection segmented from peduncle.

Antenna.—Tip of flagellum may have small spine. Antennal scale with seven plumose setae along terminal and inner margins.

Mandible.—Right mandible with five teeth between incisor and molar processes.

Maxillule.—Basipodite with five terminal spines (four slightly spinulose).

Maxilla.—Scaphognathite with 11 plumose setae on outer margin; no proximal expansion. Setation formulae of endopodite 4, 1, 3.

First and second maxillipeds.—Exopodite with seven natatory setae terminally.

Third maxilliped (Fig. 3).—Exopodite with six plumose setae terminally. Endopodite with two plumose setae terminally.

Pleopods.—May be present as minute buds.

Abdomen and telson.—Identical to Stage I except joint between somite 6 and telson indicated by small indentation in lateral margins.

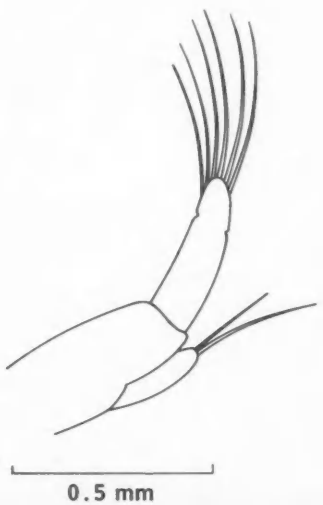


FIGURE 3.—Stage II zoea of *Rhinolithodes wosnessenskii*: third maxilliped, lateral.

DISTINCTION BETWEEN ZOEAE OF LITHODIDAE AND PAGURINAE

Zoeae of the family Lithodidae have long been considered similar morphologically to those of the subfamily Paguri nae (family Paguridae) and differ only in reduction or disappearance of the uropods (Gurney 1942; MacDonald et al. 1957). Recent descriptions of zoeae of *Cryptolithodes typicus*, *Lithodes aequispina*, *L. antarctica*, and *Paralomis granulosa* (Hart 1965; Haynes 1982; Campodonico 1971; Campodonico and Guzman 1981) have extended the range of zoeal characters of the Lithodidae and show that zoeae of the Lithodidae and Paguri nae can be distinguished by size of the eyes and morphology of the carapace and abdominal appendages (Table 1). In general, zoeae of the Lithodidae (except *Cryptolithodes typicus*) are characterized by stoutness, small eyes, posterolateral spines in middle or lower half of carapace, uniramous uropods, and no anal spine. Zoeae of the Paguri nae are characterized by slenderness, large eyes, posterolateral spines in the middle or upper half of the carapace, biramous uropods, and an anal spine. The glaucothoe of the Lithodidae and Paguri nae are readily distinguished from each other by their similarity to the adults (Haynes 1982).

TABLE 1.—Characters useful for distinguishing between zoeae of Lithodidae and zoeae of Paguri nae from the northern North Pacific Ocean. Zoeae of *Cryptolithodes typicus* (Lithodidae) are an exception and are not characterized in this table.

Lithodidae	Paguri nae
1. General appearance, stout.	General appearance, slender.
2. Longitudinal diameter of eye less than width of abdomen.	Longitudinal diameter of eye greater than width of abdomen.
3. Posterolateral spines of carapace in middle or lower half of posterior margin.	Posterolateral spines of carapace in middle or upper half of posterior margin.
4. Lateral margins of carapace nearly parallel.	Lateral margins of carapace converge posteriorly.
5. No anal spine in any stage.	Anal spine present until Stage III in some species.
6. More than eight pairs of telsonic spines in some species (excluding minute seta).	Never more than eight pairs of telsonic spines (excluding seta).
7. Uropods (when present) uniramous and terminal margin blunt with (usually three or four) short setae.	Uropods biramous; exopodite styliform terminally with usually more than three or four long setae along medial margin.

MORPHOLOGY OF LITHODID LARVAE

Lithodidae of the northern North Pacific Ocean have four zoeal stages and a glaucothoe. Stage I zoeae are characterized by sessile eyes, four natatory setae on maxillipeds 1 and 2; maxilliped 3 is undeveloped and without natatory setae; pleopods and uropods are absent; and the telson and abdominal somite 6 are fused. Beginning in Stage II, the eyes are movable, and maxillipeds have at least six natatory setae. In Stage III, undeveloped pleopods and uropods are present, and the telson and abdominal somite 6 are articulated. In Stage IV, the pleopods are biramous, and the uropods are two segmented and usually have three or four apical setae. Table 2 and the keys are provided for distinguishing described zoeae and glaucothoe of Lithodidae of the northern North Pacific Ocean. Glaucothoe of *H. grebnitzkii*, *P. wosnessenskii*, and *R. wosnessenskii* have not been described.

TABLE 2.—Characters useful for distinguishing between Stages I-IV of lithodid zoeae of the northern North Pacific Ocean. *Paralithodes brevipes* may have only three zoeal stages (Kurata 1956), thus, may not always conform to the descriptions in this table.

Characteristic	Stage I	Stage II	Stage III	Stage IV
Eyes	sessile	movable	movable	movable
Natatory setae				
First maxilliped	4	≥6	≥6	≥6
Second maxilliped	4	≥6	≥6	≥6
Third maxilliped	0	≥6	≥6	≥6
Pleopods	absent	absent	absent or present as buds	present
Uropods	absent	absent	present; unsegmented	present; two segmented
Telson and sixth abdominal somite	fused	fused	articulated	articulated

Described Lithodid Zoeae of the Northern North Pacific Ocean

1a. Carapace without posterolateral spines; uropods absent in all stages; posterior margin of telson without medial invagination ..... *Cryptolithodes typicus*

1b. Carapace with posterolateral spines; uropods present in later stages (usually Stages III and IV); posterior margin of telson with medial invagination 2

2a. Posterolateral spines of carapace short (< 1/4 carapace length) 3

2b. Posterolateral spines of carapace long (> 1/4 carapace length) 5

3a. Posterolateral spines and denticles on abdominal somites 3 and 4 about same length; posterior margins of carapace concave ..... *Hapalogaster grebnitzkii*

3b. Posterolateral spines obviously longer than denticles on abdominal somites

3 and 4; posterior margin of carapace convex 4

4a. Carapace length 1.2-1.4 mm; antennal flagellum and scale (including distal spine) about same length; antennal scale ≤5 times as long as wide ..... *Dermaturus mandtii*

4b. Carapace length 1.4-1.7 mm; antennal flagellum longer than antennal scale (including distal spine); antennal scale about 9 times as long as wide ..... *Paralithodes brevipes*

5a. Carapace with middorsal posterior spine ..... *Rhinolithodes wosnessenskii*

5b. Carapace without middorsal posterior spine 6

6a. Antennal scale with ≤6 markedly short (<1/2 scale width), lightly plumose setae ..... *Hapalogaster mertensii*

6b. Antennal scale with ≥6 long (≥1/2 scale width), heavily plumose setae 7

7a. Posterolateral spines of carapace project somewhat laterally; telson has ≥11 pairs of spines (excluding minute hair); longest (third) pair of telsonic spines fused to telson ..... *Lithodes aequispina*

7b. Posterolateral spines of carapace do not project laterally; telson has ≤8 pairs of spines (excluding minute hair); longest (third) pair of telsonic spines jointed with telson 8

8a. Spines on posterior margins of abdominal somites 2-5 markedly long and tips blunt; posterolateral spine on abdominal somite 5 blunt and sinuate ..... *Placetron wosnessenskii*

8b. Spines on posterior margins of abdominal somites 2-5 typically short and tips pointed; posterolateral spine on abdominal somite 5 pointed and not sinuate 9

9a. Telsonic spines 8 + 8 (excluding minute hair) ..... *Paralithodes platypus*

9b. Telsonic spines 7 + 7 (excluding minute hair) ..... *Paralithodes camtschatica*

Described Lithodid Glaucothoe of the Northern North Pacific Ocean. Glaucothoe of *Hapalogaster grebnitzkii*, *Placetron wosnessenskii*, and *Rhinolithodes wosnessenskii* have not been described.

1a. Dorsal surface of carapace without spines 2

1b. Dorsal surface of carapace with spines 4

2a. Carapace triangular ..... *Cryptolithodes typicus*

2b. Carapace rectangular 3

3a. Lateral margin of carapace with teeth in branchial region but not in hepatic region ..... *Hapalogaster mertensii*

3b. Lateral margin of carapace with teeth in branchial and hepatic regions ..... *Dermaturus mandtii*

4a. Tips of anterolateral spines of rostral complex spinulose; most, if not all, spines on dorsal surface of carapace bifid ..... *Lithodes aequispina*

4b. Tips of anterolateral spines of rostral complex styliform or bifid; most, if not all, spines on dorsal surface of carapace styliform 5

5a. Carapace with 15 pairs of spines on dorsal surface ..... *Paralithodes platypus*

5b. Carapace with <15 pairs of spines on dorsal surface 6

6a. Carapace with 14 pairs of spines on dorsal surface .. *Paralithodes camtschatica*

6b. Carapace with 13 pairs of spines on dorsal surface ..... *Paralithodes brevipes*

Paralithodes brevipes may have three stages; thus, Table 2 may not always be appropriate for distinguishing the stages of this species. Kurata (1956) reared and described the larvae of *P. brevipes* from ovigerous females collected in Japanese waters. In Kurata's description, *P. brevipes* has three zoeal stages instead of the four that characterize the genus, and Stage III zoeae correspond morphologically to Stage IV zoeae of the genus. Makarov (1967), however, found four zoeal stages of *P. brevipes*, including a Stage III zoea, in plankton of the west Kamchatkan coast that correspond morphologically to Stage III zoeae of the genus. Kurata's zoeae may have skipped Stage III of the genus because growing conditions in the laboratory were especially favorable (Makarov 1967).

Only Stage I zoeae of *Placetron wosnessenskii*, and Stages I and II zoeae of *Rhinolithodes wosnessenskii* have been described (this report). Because these zoeal stages are morphologically typical of lithodid species with four zoeal stages, *P. wosnessenskii* and *R. wosnessenskii* likely have the four zoeal stages characterized in Table 2.

Brief descriptions and comparisons of previously described lithodid zoeae follow.

Cryptolithodes typicus.—Based on the description by Hart (1965), *Cryptolithodes typicus* zoeae are markedly different morphologically from other described lithodid zoeae. In *C. typicus* zoeae, the carapace lacks posterolateral spines in all stages, the proximal expansion of the maxilla is present in Stage II, and the telson does not have a medial posterior invagination. In all other lithodid zoeae, the carapace has posterolateral spines in all stages, the proximal expansion of the maxilla is absent until Stage IV, and the telson has a medial posterior invagination. The large eyes of *C. typicus*, however, are typical of zoeae of the Pagurinae, and the absence of posterolateral spines on the carapace is similar to zoeae of some species of the Diogenidae. The shape of the telson, the fused abdominal somite 6 and telson in Stages III and IV, and the absence of uropods in *C. typicus* are characters similar to those of some porcellanid zoeae.

Hapalogaster grebnitzkii, *Dermaturus mandtii*, and *P. brevipes.*—Makarov (1967) briefly described larvae collected off west Kamchatka that he provisionally identified as *Hapalogaster grebnitzkii*, based on distribution of adults. Zoeae of *H. grebnitzkii* are morphologically similar to zoeae of *Dermaturus mandtii* and *Paralithodes brevipes* but can be distinguished by length of the posterolateral spines on abdominal somites 3-5. In zoeae of *H. grebnitzkii*, posterolateral spines on somites 3 and 4 are short (slightly longer than the denticles that fringe the posterior margin), and the posterolateral spines on somite 5 are shorter than the width of somite 5. In zoeae of *D. mandtii* and *P. brevipes*, posterolateral spines on somites 3 and 4 are long (at least twice the length of the denticles), and posterolateral spines on somite 5 are longer than the width of somite 5 (Kurata 1956).

Based on Kurata's (1956) brief descriptions, zoeae of *P. brevipes* can be distinguished from zoeae of *D. mandtii* by size of the carapace and morphology of the antenna. *Paralithodes brevipes* zoeae are slightly larger (carapace length, 1.4-1.7 mm) than *D. mandtii* zoeae (carapace length, 1.2-1.4 mm). The antennal flagellum of *P. brevipes* zoeae is noticeably longer than the antennal scale (including distal spine), and the antennal scale is about nine times as long as wide. The antennal flagellum and antennal scale of *D. mandtii* zoeae are about the same length, and the scale is not more than five times as long as wide.

Hapalogaster mertensii.—Larvae of *Hapalogaster mertensii* were collected from ovigerous females at Fidalgo Island, Wash., and then reared and described by Miller and Coffin (1961). Unfortunately, their description is brief and lacks detail and, therefore, has limited value. Apparently, the only characters useful for distinguishing *H. mertensii* zoeae from zoeae of other lithodid species are size and number of setae on the antennal scale. In zoeal Stages I-III of *H. mertensii*, the antennal scale has six setae and, in Stage IV, four setae. In all stages of *H. mertensii*, the setae are markedly short ($< \frac{1}{2}$ scale width) and lightly plumose. In most other lithodid zoeae, the antennal scale in Stage I has more than six heavily plumose setae that increase in number in later stages, and the setae are as long as, or longer than, the width of the antennal scale.

Lithodes aequispina.—Larvae of *Lithodes aequispina* were reared and described from ovigerous females collected in waters of southeastern Alaska (Haynes 1982). Zoeae of *L. aequispina* are most similar to zoeae of *Paralithodes camtschatica* and *P. platypus* but can be readily distinguished from their zoeae by the number of telsonic spines and the manner in which the third (longest) pair of telsonic spines is attached to the telson. In *L. aequispina*, the telson has ≥ 11 pairs of telsonic spines, and the third pair of spines is fused to the telson. In *P. camtschatica* and *P. platypus* zoeae, the telson has ≤ 8 pairs of telsonic spines, and the third (longest) pair of spines is jointed with the telson.

Paralithodes brevipes, *P. camtschatica*, and *P. platypus.*—Larvae of *Paralithodes brevipes*, *P. camtschatica*, and *P. platypus* have been described (Marukawa 1933; Kurata 1956, 1960, 1964; Hoffman 1958; Sato 1958; Makarov 1967). Zoeae of *P. brevipes* can be distinguished from zoeae of *P. camtschatica* and *P. platypus* by several characters. In *P. brevipes* zoeae, posterolateral spines on the carapace are short and ventrally curved, the dorsal posterolateral margin of the carapace is convex, the rostrum is short (about equal to the length of the antennal flagellum), and the telson has (excluding the hairlike process) six pairs of spines in Stage I and seven pairs of spines in Stages II-IV. In contrast, zoeae of *P. camtschatica* and *P. platypus* have long, posterolateral spines

on the carapace that are not ventrally curved, the dorsal posterolateral margin of the carapace is concave, the rostrum is noticeably longer than the antennal flagellum, and the number of pairs of telsonic spines in all zoeal stages (excluding the hairlike process) is 7 + 7 in *P. camtschatica* and 8 + 8 in *P. platypus*.

Placetron wosnessenskii and *Rhinolithodes wosnessenskii*.—Zoeae of *Placetron wosnessenskii* and *Rhinolithodes wosnessenskii* are readily distinguished from all other described zoeae of the Lithodidae. *Placetron wosnessenskii* zoeae are distinguished by markedly long, blunt spines on the posterior margins of abdominal somites 2-5 and the sinuate curvature of the long, blunt, posterolateral spines on abdominal somite 5. Zoeae of *R. wosnessenskii* have a spine in the middorsal, posterior margin of the carapace.

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SELECTION OF VEGETATED HABITAT BY BROWN SHRIMP, *PENAEUS AZTECUS*, IN A GALVESTON BAY SALT MARSH

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ABSTRACT

Densities of the brown shrimp, *Penaeus aztecus*, in vegetated and nonvegetated habitats of a Galveston West Bay salt marsh were compared. Each of 81 sample pairs taken between 29 March and 23 July 1982 consisted of one sample from *Spartina alterniflora* habitat and another from nonvegetated habitat. Overall a mean density for shrimp of 11.7/m² in vegetation was significantly greater than the mean density of 1.4/m² in nonvegetated habitat ($P < 0.001$, t-test, 81 paired observations). In addition, shrimp densities varied according to a pattern of lower numbers and less apparent attraction to vegetation in the outer bayside part of the marsh to that of highest numbers and greatest attraction in the innermost marsh. Accordingly, respective means for the outer, middle, and inner marsh zones in vegetated/nonvegetated sample pairs were 7.5/2.3, 11.0/1.0, and 16.6/0.6. Simple presence or absence of *S. alterniflora*, area covered by vegetation, and location within the marsh were the primary observed correlates to shrimp density patterns. Mean high water in vegetation was 22.1 cm compared with 41.8 cm for adjacent nonvegetated habitat, making vegetated habitat less accessible during periods of low water. Mechanisms that may have enhanced utilization of vegetated habitat for *P. aztecus* were reticulation in salt marsh macrostructure, relatively low tidal range, and seasonal periods of high water. The nursery function of the salt marsh was confirmed by dominance of small shrimp, with 95% of all individuals being smaller than 50 mm in rostrum through telson length. During April, the maximum mean density of postlarvae under 30 mm was 16.4/m². Recruitment of postlarvae continued throughout the summer.

A 2.8m² drop sampler, used to obtain the data, was found to be 2 to 5 times more effective for estimating densities of *P. aztecus* than trawls or seines. Consequently, our study improved the accuracy of estimates on estuarine shrimp densities, while also providing reliable evidence that *P. aztecus* may select for vegetated marsh habitat.

Estuaries have long been cited in their role as nurseries for penaeid shrimp (Anderson et al. 1949; Kutkuhn 1966; Thayer et al. 1978; Weinstein 1979). Growth and production of penaeids in estuaries have been associated with temperature (St. Amant et al. 1966; Zein-Eldin and Griffith 1966; Aldrich et al. 1968; Pullen and Trent 1969), salinity (Hildebrand and Gunter 1952; Gunter 1961; Barrett and Gillespie 1973; Browder and Moore 1981), and vegetation (Turner 1977; Faller 1979).

In salt marshes, vegetation may function variably to provide food, substrate, and protection for young penaeids. It is well known that *Spartina alterniflora* contributes to a detritus-based food web (Teal 1962; de la Cruz 1965) which at least potentially includes shrimp (Jones 1973). Microalgae and epibenthic biota associated with marshes may also serve in the food web (Haines 1977) and be used as food by foraging shrimp (Trent et al. 1969; Jones 1973). Since dense aquatic vegetation impedes certain predators (Vince et al. 1976; Nelson 1979; Coen et al. 1981; Heck and Thoman 1981), marsh grasses could also furnish protective cover for postlarval and juvenile penaeids. Unfortunately, our understanding of shrimp relationships to vegetation has been impaired by the inherent difficulty of sampling in marine vegetation.

Our aim was to overcome the sampling problem and to obtain accurate data on shrimp densities that could reliably depict differences between estuarine habitats. In the present study, *Penaeus aztecus* densities were compared between adjacent vegetated and nonvegetated habitats within a Galveston West Bay salt marsh. Since our experimental design incorporated paired sampling of habitats and samples with actual as opposed to relative numbers of shrimp, both the resolution

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and reliability of our analyses were improved over previous studies.

METHODS

Study Site

A salt marsh on the West Bay side of Galveston Island was selected as the study site (Fig. 1). The marsh extended into the island for about 2.5 km, allowing tidal circulation throughout numerous coves and bayous. The intertidal marsh was dominated by vegetation, *S. alterniflora*, and the subtidal was not vegetated. Water depth was generally <1 m, but subtidal bottom was always 10 to 20 cm deeper than adjacent intertidal vegetation. Vegetation occurred in irregular patches, creating a reticulated effect on marsh macrostructure, and occupied about 25% of the area (Fig. 2).

Experimental Design

A paired sampling design was employed to compare shrimp densities between marsh habitats. Each sample pair consisted of one sample taken in vegetated habitat and another in adjacent nonvegetated habitat as close as practically possible.

Sampling was scheduled to coincide with the

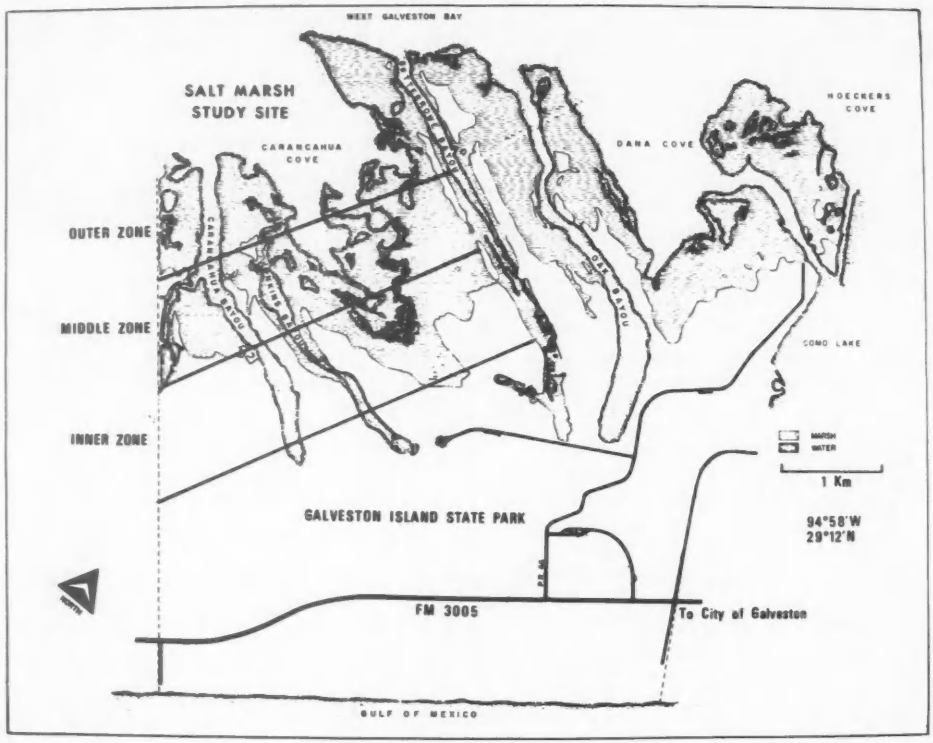

FIGURE 1.—Galveston Island State Park showing the salt marsh study site in Carancahua Cove fronting Galveston West Bay. (Redrawn from Texas Parks and Wildlife Leaflet 4000-42.)

FIGURE 2.—Upper: Reticulation between vegetated and nonvegetated habitats in a salt marsh on Galveston Island. Areal view at about 500 ft altitude. Lower: Stands of intertidal *Spartina alterniflora* and adjacent subtidal nonvegetated bottom in a salt marsh at Galveston Island State Park.

period of maximum seasonal immigration for *P. aztecus* as described by Baxter and Renfro (1967). Accordingly, seven sets of samples were taken between 29 March and 23 July 1982. Each set was obtained over a period of 3 d, and sets were taken biweekly (29 March through 28 May) and monthly (28 May through 23 July). Ordinarily, a set contained 12 sample pairs that were subdivided to sample the inner, middle, and outer marsh zones equally, i.e., during each of three sampling days four vegetated-nonvegetated sample pairs were taken from a single zone. Sample sites within zones were chosen randomly each month from subunits in a grid superimposed on a map of the area. The map and aerial photographs were used to estimate percent coverage of vegetated and nonvegetated habitats within different zones.

A *t*-test of paired observations (Steel and Torrie 1960) provided the primary means for evaluating differences in shrimp density between habitats. Other analyses were performed using Pearson product-moment correlations and ANOVAs across sample sets, and Kendall's nonparametric concordance tests (Tate and Clelland 1957) within sample sets. Analyses across sets incorporated an element of temporal variability that was specifically eliminated in analyses within sets. Data were log transformed for ANOVAs to assure homogeneity of variances.

Procedures

A drop sampler (Fig. 3) was designed to operate in the marsh from the bow of a skiff. The device was an open-ended fiber glass cylinder, reinforced on one end with galvanized metal, that enclosed 2.8 m^2 of marsh bottom. The sampler was deployed endwise and pushed at least 15 cm into the substrate to insure a good seal against leakage. After marsh grass was removed, water was pumped from the sampler and the enclosed bottom was swept with dip nets to capture the entrapped organisms. The water and the contents of the dip nets were placed into a 1 mm square mesh plankton net with a removable cod end bag. When all sample contents were washed, the cod end bag was detached, labelled, and stored in a container with Formalin[4] and Rose Bengal stain.

Two identical sampling cylinders were used to obtain sample pairs. Typically, the first sampler was hoisted above the bow of the skiff and quietly maneuvered into position over either vegetated or barren substrate. The device was released and allowed to free fall to the bottom. After disconnecting the first sampler, the second sampler was hoisted and the operation repeated in the opposing habitat. The sequence of habitats was reversed from pair to pair so that one would not continually precede the other. Sample pairs were always within two sample diameters of each other (3.6 m) and care was taken to not disturb the site until the second sampler was deployed.

Within all samples, the water temperature,

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

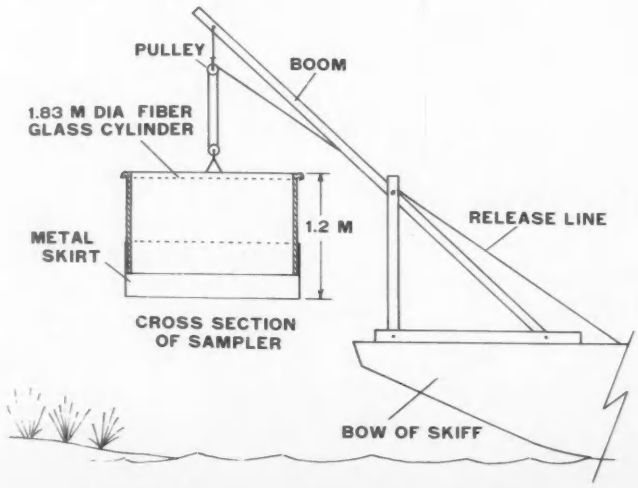

FIGURE 3.—A hand-operated drop sampler used to estimate *Penaeus aztecus* densities in a Galveston West Bay salt marsh.

oxygen (YSI oxygen meter, Model 51 B) and maximum and minimum depth were recorded. Water samples (500 ml) were also procured in order to measure turbidity (HF Instruments, Model DRT-15). In vegetated samples, emergent plant material was cut and removed to measure plant biomass and to facilitate capturing the macrofauna. Tide level was recorded from a permanent station at the beginning and end of each sampling operation. All field work was done during daylight within about 2 h before and after high tide.

In the laboratory, shrimp were identified, sorted, and measured to the nearest millimeter from rostrum tip to end of telson. Shrimp numbers for each millimeter size interval were recorded for each sample. Associated macrofauna from each sample, including fish, crabs, and other shrimp, were identified, measured, and counted. Gut contents of the fish were examined for penaeid shrimp as well as other identifiable material. Plant biomass from each sample was dried in sunlight until weight change was negligible. Sediments and epiphytes were allowed to fall away as the material dried. The resulting dry weight was taken using a Mettler K-7 toploading balance and reported as grams above-ground dry plant biomass. Stem density was calculated by weighing a subsample (about 20% of the total) and counting the number of culms.

Sampler Effectiveness

Since the experimental design assumed no sampling bias, the method was tested for recovery efficiency both in vegetated and nonvegetated habitats. Fifty shrimp, in the size range of 23 to 91 mm, were marked by clipping a uropod and placed into deployed samplers. After a 30-min adjustment period, the usual sampling procedure was followed and recovery was recorded.

Since our density data were compared with other surveys, it was useful to test the effectiveness of the drop sampler in relation to other collecting devices. These included a 1 m beam trawl, a 5.5 m bag seine, and a 3.7 m otter trawl. During the initial test, eight replicate vegetated-nonvegetated sample pairs were taken using the 1 m beam trawl (3.0 m^2) and the drop sampler (2.8 m^2). Later, 10 nonvegetated sample replicates were obtained for each of the following: the drop sampler, a 5.5 m bag seine (110 m^2), and a 3.7 m otter trawl (75 m^2). The data were reported as mean and standard deviation of shrimp density (per m^2) for each sampler. The efficiency for each device was calculated relative to the drop sampler.

RESULTS

A total of 3,277 penaeid shrimp (97% *P. aztecus*) were collected in 81 paired samples taken between 29 March and 23 July 1982. Shrimp densities in the marsh were significantly higher in *S. alterniflora* habitat than adjacent nonvegetated habitat ($P < 0.001$, t-test, 81 paired observations). The magnitude and integrity of the relationship between shrimp density and habitat type held consistently throughout all sampling dates (Table 1, Fig. 4) and zones within the marsh, except for the outer zone during March and April (Table 2). Comparison of marsh zones (Table 2) revealed highest *P. aztecus* densities and greater selection for vegetated habitat in the innermost marsh diminishing toward the outer zone. Shrimp densities in nonvegetated habitat were highest in the outer zone and diminished significantly toward the inner zone (ANOVA, $P < 0.001$).

TABLE 1.—Percent of *Penaeus aztecus* in vegetated (*Spartina alterniflora*) and nonvegetated habitats of a Galveston West Bay salt marsh, 29 March through 23 July 1982.

Sampling period	Shrimp number (n)	Habitat	
		Vegetated (% n)	Nonvegetated (% n)
3/29-4/1	355	94.4	5.6
4/13-15	519	81.7	18.3
4/26-28	802	88.3	11.7
5/11-14	309	90.3	9.7
5/26-28	388	91.8	8.2
6/22-24	237	97.0	3.0
7/21-23	559	90.2	9.8

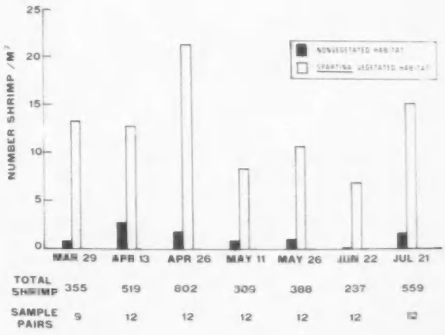

FIGURE 4.—Mean densities of *Penaeus aztecus* compared between vegetated *Spartina alterniflora* habitat and adjacent nonvegetated habitat.

TABLE 2.—Mean number of *Penaeus aztecus* per m² by zone in vegetated and nonvegetated salt marsh habitats from Galveston West Bay 29 March through 23 July 1982.

Sampling period	Marsh zone and habitat: Outer Veg/Non[1]	Middle Veg/Non	Inner Veg/Non	Overall Veg/Non
3/29-4/1	[2] 2.7/1.9 / 8.8/5.5	12.3/2.0	16.7/1.1	12.6/2.8
4/26-28	12.3/6.8	28.5/1.3	22.4/0.4	21.1/2.8
5/11-14	7.2/1.2	9.6/1.3	8.0/0.3	8.3/0.9
5/26-28	12.0/1.5	10.6/0.9	9.2/0.4	10.6/1.0
6/22-24	3.8/0.2	9.7/0.3	7.0/0.2	6.8/0.2
7/21-23	10.9/1.8	13.8/1.9	20.3/1.3	15.0/1.6
Overall	7.5/2.3	11.0/1.0	16.6/0.6	11.7/1.4

[1]Veg = *Spartina alterniflora* habitat; Non = Nonvegetated habitat.
[2]Difference within brackets not significant between vegetated and nonvegetated pairs; for all others, the difference was highly significant ($P < 0.001$, *t*-test, paired observations).

Penaeus aztecus densities for each 20 mm size interval were more abundant in *Spartina* habitat than adjacent nonvegetated bottom (Fig. 5). Vegetated habitat contained 89 to 96% of all shrimp in size classes under 50 mm and 75 to 78% of larger size classes (Table 3). Those under 30 mm in length comprised 77,% of all shrimp and those under 60 mm made up 98% of the total (Table 3). Size class distributions differed between habitats (Kolmogorov-Smirnov test, $P = 0.02$; Fig. 5), but the very small sample size from nonvegetated habitat decreased the strength of this observation.

The highest *P. aztecus* densities in vegetation and the lowest on nonvegetated bottom were characteristic of the innermost zone (Table 1). The degree of vegetated-nonvegetated differences suggested an apparent selection for vegetated habitat and greater selection in the inner zone compared with the outer zone. The increase in vegetated to nonvegetated shrimp densities coincided with an increase in *S. alterniflora* coverage between the outer and inner marsh (Fig. 6). Areal coverage of vegetation, determined from aerial photographs (Fig. 2), differed by a factor of 3 between the outer and inner marsh, and selection, as measured by the ratio of shrimp density in vegetated habitat to density in nonvegetated habitat, differed by a factor of 9 from outer to inner zones (Fig. 6). In addition, the ratio differed between the middle and inner zone, but shrimp densities within vegetation between those zones (Table 2) did not change significantly (ANOVA, Duncan's multiple range test, 0.05 level). Due to the intertidal nature of vegetated habitat, shrimp were forced into subtidal areas at low tide and redis-

TABLE 3.—Percent abundance among size classes for *Penaeus aztecus* in a Galveston West Bay salt marsh, 29 March through 23 July 1982. n = number of shrimp per size interval; N = total number of shrimp collected.

Size class (mm)	Shrimp abundance: Overall n	Overall % N	Overall Cum. %	Spartina (% n)	Nonvegetated (% n)
<20	1,117	47.7	47.7	89.4	10.6
21-30	683	29.2	76.9	95.6	4.4
31-40	234	10.0	86.9	94.9	5.1
41-50	184	7.8	94.7	88.6	11.4
51-60	86	3.7	98.4	77.9	22.1
61-70	25	1.1	99.5	76.0	24.0
71-80	6	0.3	99.8	75.0	25.0
81-90	4	0.2	100	75.0	25.0
Total (N) = 2,341					

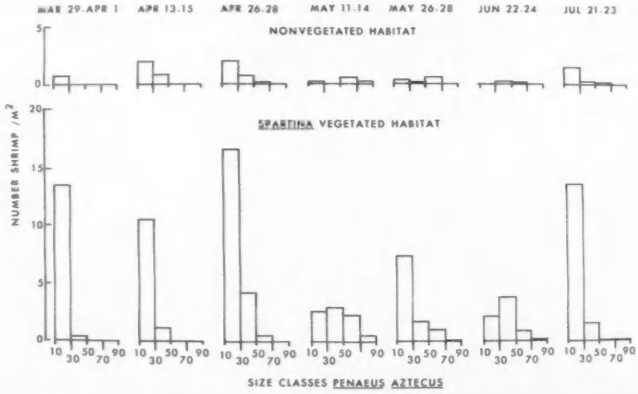

FIGURE 5.—Densities of *Penaeus aztecus* by size class in adjacent vegetated and nonvegetated habitats from Galveston West Bay during 1982. Size class distributions differed between habitats (Kolmogorov-Smirnov test, $P = 0.02$).

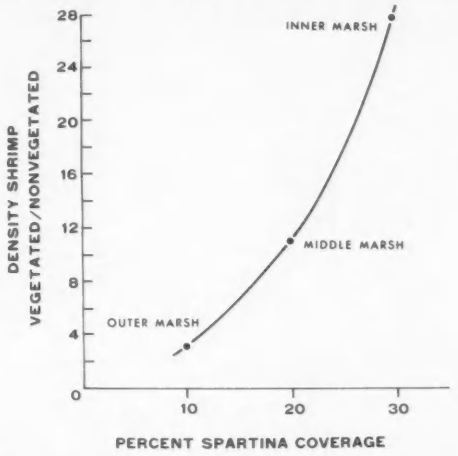

FIGURE 6.—Selection by *Penaeus aztecus* for vegetated habitat compared against percent coverage of *Spartina alterniflora*.

tributed anew on each subsequent flood tide.

Differential predation by fish did not account for shrimp differences between habitats. Of four species preying on shrimp, 328 were in vegetation versus 48 on nonvegetated bottom. Among these, 18 from vegetated (5%) and 3 from nonvegetated (6%) contained shrimp in gut contents. The predators, in order of vegetated/nonvegetated abundance, were *Lagodon rhomboides* (pinfish 246/36), *Fundulus grandis* (gulf killifish 45/0), *Cynoscion nebulosus* (spotted seatrout 22/2), and *Paralichthys lethostigma* (southern flounder 15/10). Only southern flounder contained shrimp in gut contents (3 of 10) from nonvegetated habitat. In vegetated habitat, 8 of 15 southern flounder, 10 of 22 spotted seatrout, 1 of 45 gulf killifish, and 3 of 246 pinfish contained shrimp.

Mean density of *P. aztecus* in vegetation was 11.7/m² overall with a range of 0.7 to 43.2/m² (Table 4). Densities were highest in the innermost marsh ($\bar{x}$ = 16.6/m²; range = 1.8 to 43.2/m²) and lowest in the outer marsh ($\bar{x}$ = 7.5/m²; range = 0.7 to 28.2/m²). The overall variance was less than the overall mean. Among marsh zones, shrimp patchiness in vegetation decreased slightly from the outer to inner marsh (Table 4).

Density of *P. aztecus* in nonvegetated habitat was 1.4/m² with a range of 0 to 18.2/m² (Table 4). Densities on nonvegetated bottom were highest in the outer marsh ($\bar{x}$ = 2.3/m²; range = 0 to 18.2/m²) and lowest in the inner marsh ($\bar{x}$ = 0.6/m²; range = 0 to 2.1/m²). Overall distribution on nonvegetated bottom, as reflected by the variance to mean ratio (coefficient of variation, Table 4), was patchier (more clumped) than on vegetated bottom. Shrimp distributions also were patchier in nonvegetated outer and middle zones, than in the nonvegetated inner zone.

TABLE 4.—Within habitat densities of *Penaeus aztecus* from a salt marsh in Galveston West Bay, 29 March through 23 July 1982. n = number of samples.

Marsh habitat and zone	n	Individuals/m² $\bar{x}$	Median	1 SD	Coeff. var. (%)	Range
With vegetation						
Outer	27	7.5	6.4	6.8	90	0.7-28.2
Middle	26	11.0	11.4	8.9	81	0.4-39.6
Inner	28	16.6	13.8	12.5	75	1.8-43.2
Overall	81	11.7	10.5	9.4	80	0.7-43.2
Without vegetation						
Outer	27	2.3	1.4	3.6	157	0-18.2
Middle	26	1.0	0.7	1.2	120	0- 4.6
Inner	28	0.6	1.0	1.5	56	0- 2.1
Overall	81	1.4	1.1	1.9	136	0-18.2

Stem density and above-ground biomass of *S. alterniflora* were positively correlated (Table 5). The overall range of values was 41 to 784 g/m² for biomass and 33 to 629 stems/m² with respective means of 298 g/m² (1 SD = 175, n = 81) and 234 stems/m² (1 SD = 72, n = 81). Between zones, plant biomass from the outer to inner zone increased from 258 to 348 g/m². The weight per stem increased (larger diameters) from outer to inner marsh. Although the trend suggested a negative relationship between shrimp density and vegetational density and biomass, correlation was not significant over the range examined.

Abiotic Relationships

Water depth between vegetated and nonvegetated sample pairs was significantly different ($P < 0.01$, t-test of 81 paired observations). The mean water depth was 22.1 cm (1 SD = 10.0, n = 81) in

TABLE 5.—Density and biomass of *Spartina alterniflora* from a salt marsh in Galveston West Bay, 29 March through 23 July 1982. n = number of samples.

Biomass and density	n	$\bar{x}$	1 SD	Coeff. var. (%)	Range
Biomass (g/m²)					
Outer zone	27	258	164	64	41-634
Middle zone	26	289	187	65	41-784
Inner zone	28	348	174	50	69-731
Overall	81	298	175	59	41-784
Density (stems/m²)					
Outer zone	28	234	88	38	37-576
Middle zone	26	231	65	28	33-629
Inner zone	28	236	64	27	47-496
Overall	81	234	72	31	33-629

vegetated samples compared with 41.8 cm (1 SD = 11.8, $n = 81$) in nonvegetated samples. Changes in tide level were not large (about 30 cm) but were important relative to sample depths. Since sampling was executed at high tide, tide station measurements were comparable between sampling periods and useful for establishing variability in high-water level. Mean high water during the summer was 12 cm lower than in the spring reflecting seasonally variable tidal inundation (Hicks et al. 1983) and greater accessibility to vegetation (Provost 1976) in the spring.

A weak negative relationship between shrimp density and temperature within a range of 17.0° to 34.0°C was apparent ($r = -0.34$ in vegetation, $P < 0.01$, $n = 57$). Since temperature and oxygen levels were inversely related, the trend, attributed to temperature, also extended to an observed relationship between oxygen concentration and shrimp density. However, oxygen levels were always near saturation (vegetated $\bar{x} = 8.2$ ppm, 1 SD = 1.4, $n = 81$; nonvegetated $\bar{x} = 8.1$ ppm, 1 SD = 1.4, $n = 81$) and unlikely to have influenced shrimp distribution. Shrimp densities did not correlate well with salinities (range of 19 to 35 ppt), turbidities (range of 3.0 to 55 nephelometer turbidity units), or water depths (overall range of 5.5 to 76 cm). In addition, temperature, salinity, oxygen, and turbidity did not differ between habitats (t-test of 81 paired observations for each).

Sampler Performance

Test results suggested that shrimp recovery from the drop sampler was more variable and somewhat less effective in vegetation ($\bar{x}$ = 91% recovery, 1 SD = 6.6%, $n = 4$) than in habitat without vegetation ($\bar{x}$ = 97.5% recovery, 1 SD = 2.5%, $n = 4$). However, a t-test between means by habitat revealed no significant difference ($P > 0.1$) and justified combining means (94%, 1 SD = 5.8%, $n = 8$).

Mean shrimp densities on nonvegetated bottom, comparing our 1.8 m diameter drop sampler, a 5.5 m wide bag seine, and a 3.7 m wide otter trawl, were 0.285/m², 0.104/m², and 0.054/m², respectively. Assuming 97.5% recovery and no avoidance with the drop sampler, conservative estimates of efficiency were 33% for the bag seine and 17% for the otter trawl. Clearly, the data from the drop sampler were more accurate (Table 6).

DISCUSSION

Habitat Selection

Significant differences in habitat-related shrimp densities from a Galveston salt marsh (Table 2, Fig. 4) demonstrate that *P. aztecus* may select for *S. alterniflora* habitat. In support, laboratory data of Giles and Zamora (1973) suggest that *P. aztecus* and *P. setiferus* each prefer *S. alterniflora* as opposed to barren substrate. In addition, marsh grass transplanted on a dredge spoil in Galveston Bay increased shrimp numbers (Trent et al. 1969) and elimination of marsh habitat to create waterfront housing diminished shrimp abundance (Mock 1966; Gilmore and Trent 1974; Trent et al. 1976). In other instances, *P. aztecus* has been associated with vegetation including *Ruppia* and *Vallisneria* in Mobile Bay (Loesch 1965), seagrasses in the Laguna Madre (Stokes 1974), and *Juncus*, *Spartina*, and seagrasses in Mississippi Sound (Christmas et al. 1976). The latter reported movement of postlarvae into marsh vegetation during tidal inundation.

The determinants of selection may have less to do with *S. alterniflora* per se than with other characteristics of vegetated habitat. For example, in our case, shrimp numbers were not related to the density or biomass of marsh grass (Table 5) but simply to its presence or absence. Also, attraction to vegetation differed between outer and inner marsh (Table 2). Other studies have shown that

TABLE 6.—Comparative gear efficiencies for sampling *Penaeus aztecus* in a Galveston West Bay salt marsh. Area sampled and number of replicates for each device are as follows: Drop sampler 2.8 m² ($n = 22$); beam trawl 3.0 m² ($n = 12$); bag seine 109 m² ($n = 10$); otter trawl 72 m² ($n = 10$).

Habitat type	$\bar{x}$ Efficiency			
	Drop sampler	Beam trawl	Bag seine	Otter trawl
Spartina vegetation				
(Shrimp count, $\bar{x}$/m² ±SD)	94% (8.9±3.7)	23% (2.2±2.2)	not operable	not operable
Nonvegetated				
(Shrimp count, $\bar{x}$/m² ±SD)	98% (0.30±0.3)	82% (0.25±0.46)	33% (0.10±0.06)	17% (0.05±0.04)

the presence of estuarine macrophytes can be associated with an increase in epifaunal abundance (Heck and Wetstone 1977; Heck and Orth 1980) as well as providing protective cover (Vince et al. 1976; Nelson 1979; Coen et al. 1981; Heck and Thoman 1981). For shrimp selecting vegetated marsh, this may translate into a greater variety and abundance of food and some degree of protection from predation.

Zonal and Areal Relationships

Penaeus aztecus demonstrated a greater degree of attraction to vegetated habitat in the inner than the outer marsh. Accordingly, shrimp densities were higher among vegetation and lower on nonvegetated bottom in the innermost zone compared with the outer zone. This relationship is adequately reflected by comparing ratios of vegetated with nonvegetated shrimp density. Using the ratios, the change in selection from the outer, middle, to inner zone was 3.3:1, 11.0:1, and 27.7:1, respectively. The percent area covered by *S. alterniflora* (Fig. 2) also increased (by a factor of three) from outer to inner marsh, but as vegetational coverage increased arithmetically selection by *P. aztecus* increased geometrically (Fig. 6). This implies that salt marshes with more vegetational coverage have disproportionately greater attractive value to *P. aztecus* than do those with less coverage. On a larger scale, Turner (1977) revealed a positive correlation between extensiveness of estuarine vegetation and offshore shrimp yield. However, the relationship may not be simple; it is likely to depend upon characteristics such as the configuration, accessibility, and quality of vegetational patches within a marsh. For instance, an edge effect has been identified which associates large numbers of shrimp with the nonvegetated zone adjacent to vegetation (Mock 1966; Christmas et al. 1976). Since our *Spartina* habitat was intertidal, and often not inundated during low tides, the nonvegetated subtidal habitat provided a refuge against stranding. We have assumed that it did and that shrimp redistributed accordingly each tidal cycle. It is evident that an increase in the amount of ecotone edge (between habitats) would facilitate movement for the shrimp population. It is also evident that the amount of edge is proportionally related to the degree of reticulation in the marsh (Fig. 2). Thus, reticulation may be an important mechanism for increasing the accessibility of intertidal vegetation to *P. aztecus*.

Shrimp Densities

Density estimates for penaeid shrimp in *S. alterniflora* vegetation have not been reported previously. We found a density range for *P. aztecus* in *Spartina* habitat of 0.7 to 43.2/m² with an overall mean, from March through July, of 11.7/m² (1 SD = 9.4, n = 81). Comparable densities from adjacent nonvegetated habitat ranged between 0 and 18.2/m². All densities were taken when *P. aztecus* numerically dominated the shrimp population. By August, when *P. setiferus* first began to dominate, the combined mean for both species in vegetation increased to 50.8/m² (1 SD = 31.6, n = 12) and a single sample attained a density of 118.6 shrimp/m². These data may indicate a potential for higher *P. aztecus* densities earlier in the season and suggest that *P. aztecus* were not restricted by lack of space.

To our knowledge, we have provided the first accurate estimates of shrimp density in marsh vegetation, and our densities are among the few available for any estuarine system. Due to method limitations, most researchers have only reported relative abundances of restricted sizes, usually over nonvegetated bottom. The single exception was data by Allen and Hudson (1970), using a suction sampler in seagrasses in Florida Bay. From 43 trials, they reported a mean of 6.2/m² ± 3.4 SD for *P. duorarum*.

Estimates of *P. aztecus* densities from nonvegetated bottom in three other Galveston Bay salt marshes were available from the Texas Parks and Wildlife Department (TPWD) from 1976 through 1981 (Benefield 1982, footnote 5.). The data were taken using a marsh net (Renfro 1963) which was relatively effective for capturing shrimp on nonvegetated bottom (Table 6 compares a beam trawl, similar to the marsh net, with other sampling devices). Mean TPWD densities for *P. aztecus* during the latter half of March were 10.4/m² for 1976, 5.2/m² for 1977, 0.3/m² for 1978, 1.3/m² for 1979, 8.7/m² for 1980, and 5.1/m² for 1981 with an overall mean of 5.2/m². In our study, on nonvegetated bottom, the March mean for *P. aztecus* was 0.9/m² and overall (March through July) the mean was 1.4/m². It is evident that our nonvegetated densities for *P. aztecus* were within the range, but low compared with the mean calculated from TPWD data.

These densities of *P. aztecus* may not be strictly

[5]R. L. Benefield, Bay Shrimp Project Leader, Texas Parks and Wildlife Department, Coastal Fisheries Branch, P.O. Box 8, Seabrook, TX 77586, pers. commun. September 1982.

comparable, since sampling was executed during unknown variable tidal stages and the degree of flooding in intertidal vegetation appears to greatly influence shrimp densities on nearby nonvegetated subtidal bottom. Perhaps the only meaningful density estimates are those taken during low tide in nonvegetated habitat or those taken in vegetated habitat at flood tide. In any case, tide stage must be uniform for data to be comparable.

Sampling Integrity

The sampling approach in our investigation provided more realistic density estimates than traditional methods for sampling shrimp in estuaries (Table 6). We agree with Loesch et al. (1976) in concluding that techniques such as the area-swept method using an otter trawl are among the poorest for quantifying *P. aztecus*. Past recognition of this problem stimulated development of the push net (Allen and Inglis 1958), small beam trawl (Renfro 1963; Loesch 1965), and marsh net (Pullen et al. 1968). These samplers improved accuracy on nonvegetated bottom, but were ineffective when vegetation was present and did not solve avoidance problems. Further improvement came for sampling in seagrasses, but not salt marshes, with the invention of a sled-mounted suction sampler (Allen and Hudson 1970) and modification of a drop net technique (Hoese and Jones 1963; Gilmore et al. 1976). Our methodology has been designed to minimize escape, improve recovery from the area sampled (including burrowed shrimp), and to operate in salt marsh habitats. The drop-sampler method proved to be nearly as effective among vegetation as on nonvegetated bottom.

CONCLUSION

We contend that differences in *P. aztecus* densities between vegetated and nonvegetated marsh bottom were due to habitat selection. In support, we refer to Loesch (1965), Trent et al. (1969), and Stokes (1974) who have associated brown shrimp distributions with estuarine vegetation, and a laboratory experiment by Giles and Zamora (1973) demonstrating *P. aztecus* prefer *S. alterniflora* instead of barren substrate. Finally, our fish gut examinations indicate that immediate effects of predation did not account for the density differential.

Since *S. alterniflora* is characteristically intertidal, and not continuously available to shrimp, the adjacent subtidal zone provided an important alternate habitat during low tide. We propose that the amount of edge between habitats facilitated shrimp movement, and the reticulated nature of the salt marsh was an important feature for increasing the amount of edge. In addition, intertidal vegetation was more accessible and its potential for utilization greater during spring and fall high tides. This interaction may in part account for seasonal peaks in *P. aztecus* populations. In our investigation, recruitment began abruptly with equinox tides. The shrimp population during the spring and early summer was dominated entirely by *P. aztecus*.

Our shrimp densities from vegetated habitat were higher than any previously reported including those from seagrass and mangrove systems. The high densities in vegetation were possibly governed by the amount of total marsh, ratio of vegetated to nonvegetated habitat, and size of recruitment. The densities on nonvegetated marsh bottom were probably controlled by the relative accessibility of nearby vegetated habitat. In any case, the observed density differential strongly implies that marsh vegetation provides a vital function for juvenile brown shrimp.

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REPRODUCTION, MOVEMENTS, AND POPULATION DYNAMICS OF THE BANDED DRUM, *LARIMUS FASCIATUS*, IN THE GULF OF MEXICO[1, 2]

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ABSTRACT

Collections of banded drum, *Larimus fasciatus*, were made from 5 to 100 m in the Gulf of Mexico along a cross-shelf transect off Texas during the period October 1977-August 1981. *Larimus fasciatus* mature at 80-130 mm as they approach age I. Spawning occurs during two discrete periods, a major fall period (September-November) and a very minor spring period (April-June), coincident with downcoast alongshore currents (toward Mexico) and onshore surface Ekman transport. Fish first spawning at 12-14 months old produce the predominant fall-spawned groups. Fall-spawned fish spawning at 19-21 months old produce the minor spring-spawned groups, so that temporal reproductive isolation does not exist between spring and fall cohorts. *Larimus fasciatus* in the northwestern Gulf range from <5 to 55 m but are most abundant at 5-16 m. Adults occupy the 13-24 m bathymetric range, while the young recruit in waters of <5-16 m when 2-4 months old. Larger, older, spawning or postspawning individuals may undergo more or less permanent emigration from the northwestern Gulf to the north central area as they approach age I. Apparent mean sizes of fall-spawned fish were 130-150 mm at age I and 155-180 mm at or approaching age II. Von Bertalanffy parameters for fall-spawned fish were 201 and 176 mm for L_∞ and 1.15 and 1.34 for K (annual), respectively. Maximum size is about 180 mm in the northwestern Gulf, but more typically only 160-165 mm. Typical maximum life span (t_L) in the northwestern Gulf is only 1-2 years but may be 2-3 years if the the stock ranges in both the northwestern and north central Gulf. Apparent mean time-specific and cohort-specific total annual mortality rates are 92-100% in the northwestern Gulf but true values probably are 80-90% for a stock that ranges in both the northwestern and north central Gulf. Fecundity, weight, girth, and length relationships are presented.

The banded drum, *Larimus fasciatus*, is a common demersal fish that ranges along the Altantic coast of the United States from Chesapeake Bay to southern Florida and in the Gulf of Mexico (Gulf) from the west coast of Florida to Campeche Bay (Hildebrand and Schroeder 1928; Hildebrand 1954; Briggs 1958). It primarily occurs in nearshore marine waters (Hildebrand and Cable 1934; Powles 1980) and only occasionally enters the lower reaches of estuaries (Gunter 1938; Swingle 1971; Dahlberg 1972). In the northern Gulf this species is most abundant off Louisiana (Gunter 1945; Behre 1950; Hildebrand 1954).

The life history of *L. fasciatus* is poorly known despite its common occurrence. No detailed study describes its life history in the Gulf, although Ross (1978) did so for North Carolina. Life history notes appear in Hildebrand and Cable (1934), Miller and Jorgenson (1969), Christmas and Waller (1973), Chao and Musick (1977), Johnson (1978), and Powles (1980).

This paper describes maturation, spawning periodicity, bathymetric distribution, recruitment, movements, age determination and growth using length frequencies, maximum size, life span, mortality, sex ratios, fecundity, and length-weight, length-girth, and standard-total length relationships of *L. fasciatus* in the northwestern Gulf.

METHODS

Larimus fasciatus were collected in 71 monthly or twice monthly cruises from October 1977 through August 1981 along a transect in the Gulf off Freeport, Tex., (Fig. 1) aboard a chartered shrimp trawler using twin 10.4 m (34-ft) trawls with a 4.4 cm stretched mesh cod end and a tickler chain. Initial stations usually were located at depths of 9, 13, 16, 18, 22, 27, 36, and 47 m. Sampling was expanded to include stations at 5 and 24

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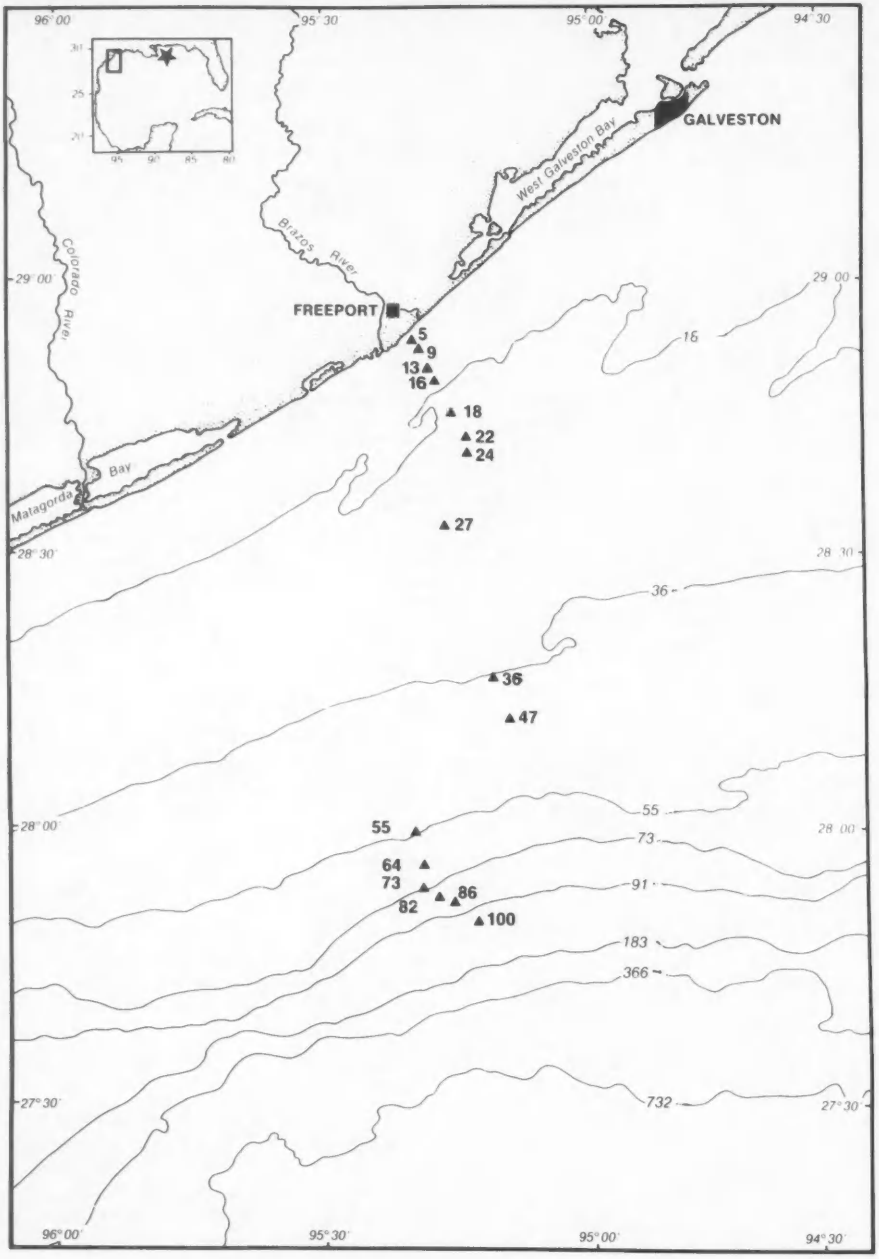

FIGURE 1.—Location of sampling area off Freeport, Tex. Station depths and bathymetric contours are indicated in meters. Starred area in insert indicates where collections were made in the north central Gulf.

m after November 1978 and at 55, 64, 73, 82, 86, and 100 m after May 1979. Collections were made during the day through September 1978; thereafter, a day and a night cruise usually were made each month. Two 10-min tows (bottom time) were made at each depth except that 1 tow was made at most depths prior to October 1978, usually 8 tows were made at 16 m, and usually 24 tows were made at 22 m.

All *L. fasciatus* were culled from the catch, measured to the nearest millimeter total length, fixed in 10% Formalin[5], and later preserved in 70% ethanol. For the period October 1979-April 1981, if available, 300 fish each month were selected for intensive processing using stratified random sampling in which a stratum included an individual spawned group (Standard 1983: app. 1). The following data were taken on the first 200 fish selected: total length (TL), standard length (SL), girth at origin of dorsal fin (G), total weight (TW), gonad weight (GW), sex, and ovary maturity stage. Only sex and ovary maturity stage were recorded for the remaining 100 fish. Maturity stages (Table 1) were assigned to immature and female fish using a slight modification of Kesteven's system (Bagenal and Braum 1971). Gonadosomatic indices (GSI) were calculated for individual females as GSI = 100 GW/TW.

Supplemental collections were made in the north central Gulf from 24 October to 5 November 1982 aboard the FRS *Oregon II* (NMFS) using standard 12.2 m (40-ft) 4-seam semiballoon shrimp trawls at depths of 9-91 m between long. 88°00′ and 89°00′W and at depths of 347-549 m between long. 87°50′ and 88°00′W (Rohr et al.[6]). Total length was measured on all *L. fasciatus* captured to compare with size compositions from the northwestern Gulf.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Description of gonad maturity stages assigned to *Larimus fasciatus*.

Stage and name	Description
1 Immature	Gonads barely or not visible, sexes indistinguishable to the naked eye.
2 Maturing Virgin	Ovaries small, thin, confined to posteriodorsal wall of body cavity.
3 Early Developing	Ovaries solid, opaque, occupy <30% of body cavity. Individual eggs not visible to naked eye.
4 Late Developing	Ovaries occupy >30% of body cavity. Individual eggs opaque, distinguishable to naked eye by close examination.
5 Gravid	Ovaries occupy >50% of body cavity. Individual eggs distinct, <50% translucent.
6 Ripe	Ovaries completely fill body cavity, >50% of the eggs translucent.
7 Spawning/Spent	Ovaries flaccid, remaining eggs translucent.
8 Resting	Ovaries firm, occupy <30% of body cavity, translucent eggs may persist. Fish large enough to have spawned.

Age in years was determined by length-frequency analysis, e.g., the Petersen Method (Lagler 1956). Spawned groups (intrayear class cohorts) were specified by the season and year when they hatched, e.g., fall 1980. Descriptions of spawning periodicity (beginnings and ends) using length frequencies assume the following size and age combinations predicted from quadratic regression of total length on age, years pooled, noted below: 15 mm TL at 1 mo, 30 mm at 2 mo, and 45 mm at 3 mo. The same combinations were predicted from regressions for individual fall-spawned groups.

Duration of the spawning period was approximated for fall-spawned groups following Geoghegan and Chittenden (1982) as

$$\frac{\text{Time-specific mean size range early in life}}{\text{Mean growth/day early in life}}.$$

Calculations were based on April-June data, the first months when fall groups appeared fully recruited. Time-specific size range was estimated for each fall group as the mean of the 99% confidence intervals for observations in April-June (Table 2). Growth per day was estimated as the mean of the growth per day values between successive collections in the April-June period (Table 2). This procedure assumes large fish hatch before small ones and that all grow at the same rate (Geoghegan and Chittenden 1982). The latter assumption appears valid because 99% confidence intervals for observations (Table 3) were fairly constant within cruises in the April-June period when sample sizes were large.

Hatching dates used to set time scales to calculate growth of fall-spawned fish were determined by a one-step iteration process. A hatching date of 1 October was assigned to start the process because 1) fish 20-40 mm TL, which we assumed were 1-3 mo old, first appear in November-December, and 2) slopes for regressions of ovary weight on total length (Fig. 2) and mean GSI (Fig. 3) were greatest in September-October. Quadratic regressions of total length on age in days were then used as a simple model to estimate initial x-intercepts for each fall-spawned group. Final hatching dates

[6]Rohr, B. A., A. J., Kemmerer, and W. H. Fox, Jr. 1983. FRS *Oregon II* Cruise 130, 10-12-11/24/82. Cruise Rep., 22 p. Southeast Fisheries Center Pascagoula Facility, National Marine Fisheries Service, NOAA, P.O. Drawer 1207, Pascagoula, MS 39567-0112.

TABLE 2.—Calculations (see Methods) to estimate duration of fall spawning periods of *Larimus fasciatus* during 1977, 1978, 1979, and 1980. Collection dates, sample sizes, means, and 99% confidence limits for observations were obtained from Table 3.

Group and collection date	*n*	Mean total length	99% confidence limits of observations	Growth increment between first and last date	Time (days)	Growth/Day (mm)
1977 fall-spawned group						
14 Apr. 1978	5	69.0	33.9-104.0	18.5	24	0.77
8 May 1978	37	87.5	63.9-111.1			
Means			58.65 (interval)	18.5	24	0.77
Spawning period = 58.65/0.77 = 76 d						
1978 fall-spawned group						
5 Apr. 1979	197	67.6	39.3-95.9	11.1	15	0.74
20 Apr. 1979	328	78.7	50.6-106.8	16.1	24	0.67
14 May 1979	490	94.8	68.0-121.6	20.5	23	0.89
6 June 1979	65	115.3	85.3-145.3	7.1	15	0.47
21 June 1979	151	122.4	104.0-140.8			
Means			52.64 (interval)	13.7	19	0.69
Spawning period = 52.64/0.69 = 76 d						
1979 fall-spawned group						
1 Apr. 1980	746	72.6	49.3-95.9	7.0	15	0.47
16 Apr. 1980	437	79.6	53.1-106.0	0.1	19	0.01
5 May 1980	1,202	79.7	55.2-104.2	9.1	14	0.65
19 May 1980	239	88.8	59.8-117.8	15.0	14	1.07
2 June 1980	614	103.8	81.3-126.3	12.1	17	0.71
19 June 1980	254	115.9	90.2-141.6			
Means			50.48 (interval)	8.7	16	0.58
Spawning period = 50.48/0.58 = 87 d						
1980 fall-spawned group						
7 Apr. 1981	110	60.0	33.1-86.9	14.2	13	1.09
20 Apr. 1981	69	74.2	45.7-102.7	6.2	14	0.44
4 May 1981	97	80.4	57.0-103.8	9.3	15	0.62
18 May 1981	165	89.7	68.8-110.6	12.8	14	0.91
2 June 1981	128	102.5	77.9-127.1	9.3	13	0.72
15 June 1981	174	111.8	90.4-133.2	10.4	14	0.76
Means			48.57 (interval)			
Spawning period = 48.57/0.76 = 64 d						

TABLE 3.—Growth data (mm TL) by spawned group for *Larimus fasciatus* from the Gulf off Freeport, Tex. Night and day cruises are indicated by night (N) and day (D). Observed size ranges delineate spawned group boundaries used in growth and mortality calculations and indicated in Figure 6. Collection dates with asterisks indicate collections pooled to estimate mean size at age.

Group and collection date		*n*	Observed size range (mm)	Mean length (mm)	s^2	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
1976 fall-spawned group								
1 Oct. 1977	D*	9	120-143	133.6	46.5	128.4-138.8	110.7-156.5	+ 4.9
3 Dec. 1977	D	2	136-141	138.5	12.5	106.7-170.3	−86.6-363.6	
1977 fall-spawned group								
21 Mar. 1978	D	10	47-97	62.3	261.3	50.7-73.9	9.8-114.8	+ 6.7
14 Apr. 1978	D	5	62-78	69.0	58.0	59.5-78.5	33.9-104.0	+18.5
8 May 1978	D	37	70-104	87.5	75.0	84.6-90.4	63.9-111.1	+40.0
15 July 1978	D	286	113-141	127.5	26.5	126.9-128.1	114.2-140.8	+20.5
15 Sept. 1978	D*	8	145-152	148.0	8.6	145.5-150.5	137.7-158.3	+ 1.2
1 Dec. 1978	N	14	141-162	149.2	33.3	145.9-152.5	131.8-166.6	+ 5.8
13 Dec. 1978	D	1	155	155.0	—	—	—	+ 1.0
6 June 1979	N	1	156	156.0	—	—	—	+18.0
21 June 1979	D	1	174	174.0	—	—	—	
1978 fall-spawned group								
1 Dec. 1978	N	98	34-99	64.3	220.7	61.3-67.3	25.3-103.3	+ 9.5
13 Dec. 1978	D	51	34-98	73.8	266.6	69.2-78.4	30.1-117.5	− 7.5
24 Feb. 1979	D	19	40-97	66.3	343.8	57.4-75.2	12.9-119.7	+ 1.3
5 Apr. 1979	N	197	45-98	67.6	120.3	66.1-69.1	39.3-95.9	+11.1
20 Apr. 1979	D	328	51-115	78.7	118.7	77.5-79.9	50.6-106.8	+16.1
14 May 1979	N	490	68-134	94.8	108.0	93.9-95.7	68.0-121.6	+20.5
6 June 1979	N	65	78-130	115.3	128.1	112.5-118.1	85.3-145.3	+ 7.1
21 June 1979	D	151	95-140	122.4	51.3	121.3-123.5	104.0-140.8	− 1.4
5 July 1979	N	3	115-131	121.0	76.0	99.3-142.7	34.5-207.5	+ 2.5
19 July 1979	D	83	111-138	123.5	42.7	122.1-124.9	106.3-140.7	+15.6
22 Aug. 1979	D	83	111-155	139.1	54.5	137.5-140.7	119.6-158.6	+ 5.7
22 Sept. 1979	D*	23	132-164	144.8	38.8	142.1-147.5	127.2-162.4	+ 0.8
2 Oct. 1979	N*	59	133-156	145.6	29.8	144.2-147.0	131.1-160.1	− 1.5
16 Oct. 1979	D*	198	127-164	144.1	34.6	143.3-144.9	128.9-159.3	+ 2.0
3 Nov. 1979	N	9	138-158	146.1	43.4	141.0-151.2	124.0-168.2	+ 2.8
15 Nov. 1979	D	7	144-155	148.9	13.8	145.5-152.3	135.1-162.7	+ 2.8

TABLE 3.—*Continued*

Group and collection date		*n*	Observed size range (mm)	Mean length (mm)	s^2	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
1 Dec. 1979	N	3	148-155	151.7	12.3	143.0-160.4	116.9-186.5	
14 Dec. 1979	D	1	163	163.0	—	—	—	+11.3
3 Jan. 1980	N	1	157	157.0	—	—	—	− 6.0
4 Feb. 1980	N	1	146	146.0	—	—	—	−11.0
5 Mar. 1980	N	1	150	150.0	—	—	—	+ 4.0
19 Mar. 1980	D	45	135-163	151.8	29.8	150.2-153.4	137.1-166.5	+ 1.8
16 Apr. 1980	D	8	132-166	150.5	91.4	142.5-158.5	117.0-184.0	− 1.3
19 May 1980	D	2	161-182	171.5	220.5	38.1-304.9	−773.8-1,116.8	+21.0
2 June 1980	N	22	146-174	158.5	37.4	155.8-161.2	141.2-175.8	−13.0
19 June 1980	D	26	147-180	157.2	50.8	154.3-160.1	137.3-177.1	− 1.3
7 July 1980	N	45	150-172	159.2	26.1	157.7-160.7	145.4-173.0	− 2.0
5 Aug. 1980	N*	11	156-175	163.3	31.6	159.5-167.1	145.5-181.1	+ 4.1
7 Sept. 1980	N*	1	177	177.0	—	—	—	+13.7
1979 fall-spawned group								
3 Nov. 1979	N	4	21-41	32.5	70.3	19.2-45.8	−16.5-81.5	
15 Nov. 1979	D	2	36-45	40.5	40.5	−16.7-97.7	−364.6-445.6	+ 8.0
1 Dec. 1979	N	24	33-87	55.3	269.6	48.4-62.2	9.2-101.4	+14.8
14 Dec. 1979	D	74	29-88	50.8	146.4	48.0-53.6	18.8-82.8	− 4.5
3 Jan. 1980	N	39	34-110	56.6	313.2	50.9-62.3	8.7-104.5	+ 5.8
16 Jan. 1980	D	246	31-124	54.1	108.8	52.8-55.4	27.2-81.0	− 2.5
4 Feb. 1980	N	581	33-109	58.1	99.2	57.3-58.9	32.4-83.8	+ 4.0
15 Feb. 1980	D	1723	30-97	60.1	77.3	59.7-60.5	37.5-82.7	+ 2.0
5 Mar. 1980	N	507	39-95	61.0	80.5	60.2-61.8	37.9-84.1	+ 0.9
19 Mar. 1980	D	217	47-121	71.9	103.5	70.5-73.3	45.7-98.1	+10.9
1 Apr. 1980	N	746	45-115	72.6	81.7	72.0-73.2	49.3-95.9	+ 0.7
16 Apr. 1980	D	437	44-108	79.6	105.1	78.6 80.6	53.1-106.0	+ 7.0
5 May 1980	N	1202	54-114	79.7	90.5	79.2-80.2	55.2-104.2	+ 0.1
19 May 1980	D	239	59-116	88.8	127.1	87.4-90.2	59.8-117.8	+ 9.1
2 June 1980	N	614	72-139	103.8	76.5	103.1-104.5	81.3-126.3	+15.0
19 June 1980	D	25	86-139	115.9	99.6	114.7-117.1	90.2-141.6	+12.1
7 July 1980	N	750	90-149	120.5	84.2	119.8-121.2	96.9-144.1	+ 4.6
21 July 1980	D	142	104-153	124.3	84.6	122.8-125.8	100.6-148.0	+ 3.8
5 Aug. 1980	N	794	102-155	130.9	73.0	130.3-131.5	108.9-152.9	+ 6.6
26 Aug. 1980	D	1	157	157.0	—	—	—	+26.1
7 Sept. 1980	N*	116	123-158	146.0	42.1	144.8-147.2	129.0-163.0	−11.0
22 Sept. 1980	D*	12	143-162	151.7	39.2	147.7-155.6	132.3-171.1	+ 5.7
6 Oct. 1980	N*	82	137-168	148.7	36.7	147.4-150.0	132.7-164.7	− 3.0
20 Oct. 1980	D*	5	118-156	141.0	251.0	121.3-160.7	48.5-233.5	− 7.7
3 Nov. 1980	N	27	140-173	152.9	67.1	149.7-156.1	130.1-175.7	+11.9
18 Nov. 1980	D	18	143-157	151.9	14.6	150.0-153.8	140.8-163.0	− 1.0
1 Dec. 1980	N	4	149-153	151.5	3.7	148.4-154.6	140.3-162.7	− 0.4
15 Dec. 1980	D	1	147	147.0	—	—	—	− 4.5
7 Jan. 1981	N	7	127-167	143.0	211.7	129.5-156.5	89.1-196.9	− 4.0
2 Feb. 1981	N	1	157	157.0	—	—	—	+14.0
16 Feb. 1981	D	2	130-150	140.0	200.0	12.9-267.1	−760.2-1,040.2	−17.0
7 Apr. 1981	N	2	145-146	145.5	0.5	139.1-151.9	100.5-190.5	+ 5.5
20 Apr. 1981	D	3	133-148	141.0	57.0	122.2-159.8	66.1-215.9	− 4.5
4 May 1981	N	20	148-167	155.8	23.5	153.5-158.1	141.9-169.7	+14.8
2 June 1981	N	5	143-161	153.0	43.5	144.8-161.2	122.6-183.4	− 2.8
15 June 1981	D	11	146-174	159.0	53.2	154.1-163.9	135.9-182.1	+ 6.0
1 July 1981	N	9	143-171	159.0	85.0	151.9-166.1	128.1-189.9	0.0
20 July 1981	D	199	146-176	158.5	40.5	157.6-159.4	142.1-174.9	− 0.5
1980 spring-spawned group								
3 Aug. 1980	N	7	58-80	65.4	64.0	58.0-72.8	35.7-95.1	
1980 fall-spawned group								
18 Nov. 1980	D	1	68	68.0	—	—	—	
1 Dec. 1980	N	62	22-108	52.6	267.0	48.4-56.8	15.0-90.2	−15.4
15 Dec. 1980	D	2	29-36	32.5	24.5	−12.0-77.0	−282.6-347.6	−20.1
7 Jan. 1981	N	191	31-91	52.1	231.2	49.9-54.3	12.9-91.3	+19.6
21 Jan. 1981	D	25	33-82	54.3	214.0	48.3-60.3	13.4-95.2	+ 2.2
2 Feb. 1981	N	255	21-118	46.8	93.7	45.6-48.0	21.9-71.7	− 7.5
16 Feb. 1981	D	49	33-108	62.1	330.2	56.9-67.3	13.4-110.8	+15.3
2 Mar. 1981	N	32	42-86	55.7	156.5	51.2-60.2	21.4-90.0	− 6.4
16 Mar. 1981	D	11	43-87	56.2	129.8	48.5-63.9	20.1-92.3	+ 0.5
7 Apr. 1981	N	110	39-87	60.0	105.7	58.1-61.9	33.1-86.9	+ 3.8
20 Apr. 1981	D	69	56-107	74.2	115.7	71.6-76.8	45.7-102.7	+14.2
4 May 1981	N	97	64-107	80.4	79.7	78.6-82.2	57.0-103.8	+ 6.2
19 May 1981	D	165	70-115	89.7	66.0	88.5-90.9	68.8-110.6	+ 9.3
2 June 1981	N	128	78-129	102.5	91.1	100.8-104.2	77.9-127.1	+12.8
15 June 1981	D	174	92-133	111.8	68.8	110.6-113.0	90.4-133.2	+ 9.3
1 July 1981	N	46	106-137	120.2	39.8	118.4-122.0	103.3-137.1	+ 8.4
20 July 1981	D	152	107-145	133.2	41.8	132.2-134.2	116.5-149.9	+13.0
3 Aug. 1981	N	132	120-166	141.5	62.0	140.2-142.8	121.2-161.8	+ 8.3
16 Aug. 1981	D	428	105-170	143.3	49.3	142.6-144.0	125.2-161.4	+ 1.8
1981 spring-spawned group								
15 June 1981	D	2	42-47	44.5	12.5	12.7-76.3	−180.6-269.6	
20 July 1981	D	9	41-72	54.0	110.8	45.9-62.1	18.7-89.3	+ 9.5
3 Aug. 1981	N	2	58-79	68.5	220.5	−64.9-201.9	−876.8-1,013.8	+14.5

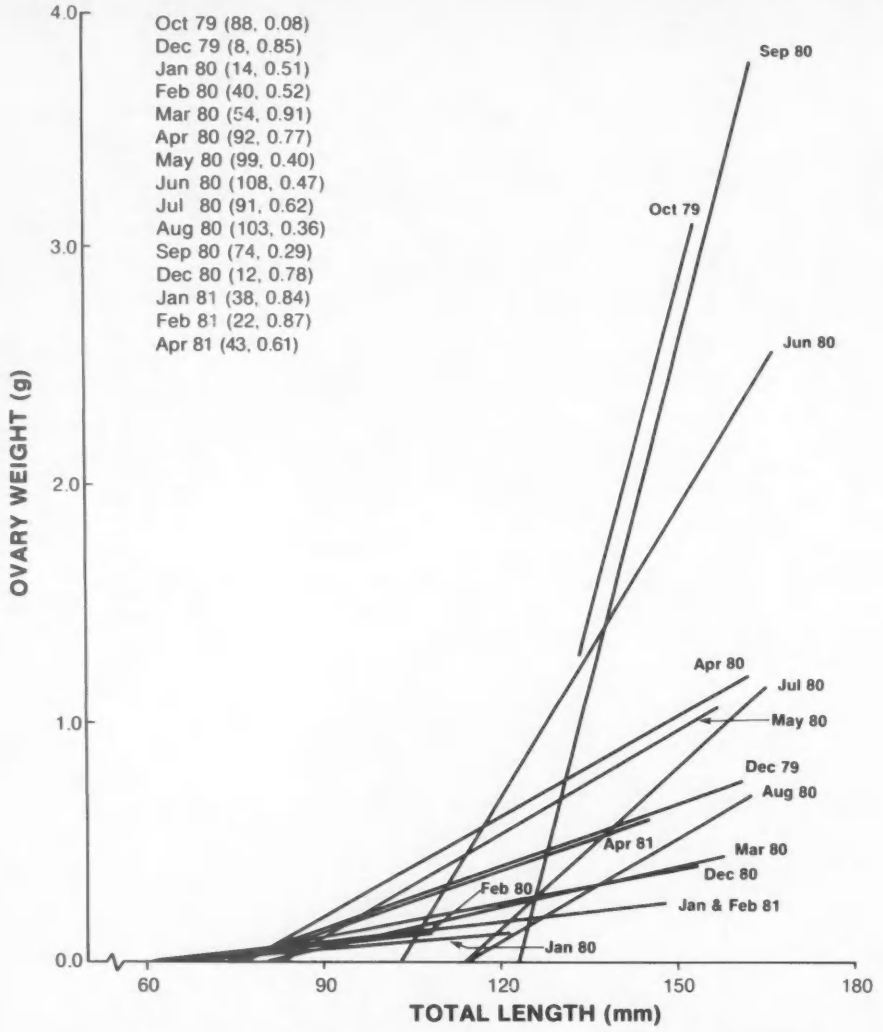

FIGURE 2.—Monthly regressions of ovary weight on total length for *Larimus fasciatus*. Length of each line shows the observed size range. Sample sizes and r^2 values are tabulated for each period. Regressions presented were significant at $\alpha = 0.05$.

were calculated by using initial x-intercepts to readjust the initial x-variable (time) scale, so that each final growth curve passed through the origin (Table 4). Final calculated hatching dates are mean values because regressions predict averages. Rate parameters—e.g., regression coefficients, growth/30 d, and von Bertalanffy K values—fitted to observed size data are the same within rounding error regardless of the hatching dates used, because curves are fitted to the same time dimension between the initial and last collection of a cohort.

Total annual mortality rates ($1 - S$) were calculated on a time-specific and cohort-specific basis from the expression $S = N_t/N_0$ where S = rate of survival, and N_t and N_0 are the numbers of fish at

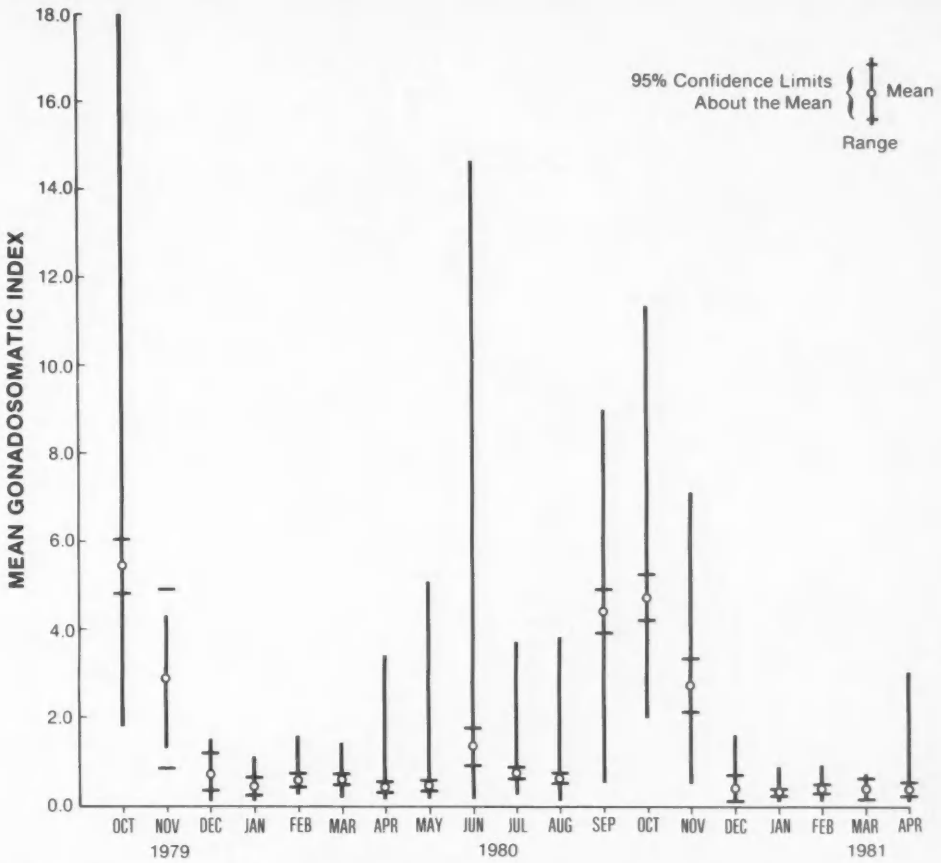

FIGURE 3.—Monthly mean gonadosomatic indices, ranges, and 95% confidence limits about means for female *Larimus fasciatus*, spawned groups pooled, October 1979-April 1981.

TABLE 4.—Summary of iterative process used to calculate final hatching dates and set time scales for growth calculations. Equations describe regressions of observed mean total length (TL) on age in days. Initial age values and growth equations were scaled to a 1 October hatching date. Final fitted regressions are in Figure 7.

Spawned group	Initial growth equation	Initial *x*-intercept	Final growth equation	Final calculated hatching date
Fall 1978	$y = 28.59 + 0.40825x - 0.00031x^2$	−67	$y = -0.13 + 0.44924x - 0.00031x^2$	27 July 1978
Fall 1978, initial two collections deleted	$y = -8.28 + 0.58365x - 0.00049x^2$	14	$y = -0.21 + 0.56983x - 0.00049x^2$	15 Oct. 1978
Fall 1979	$y = 7.41 + 0.51937x - 0.00045x^2$	−14	$y = 0.13 + 0.53162x - 0.00045x^2$	17 Sept. 1979
Fall 1980	$y = 12.94 + 0.36704x$	−35	$y = 0.09 + 0.36704x$	27 Aug. 1980
Fall 1980, initial two collections deleted	$y = -7.47 + 0.45303x$	16	$y = -0.22 + 0.45303x$	17 Oct. 1980

age each month. Analyses excluded several months in which estimates were not reliable because of incomplete recruitment (2 mo, time-specific; 6 mo, cohort-specific), seeming immigration (1 mo, time-specific), or some stations were not occupied in one cruise (1 mo, cohort-specific). Pooled estimates of S were calculated using Heincke's procedure (Ricker 1975) and were converted to $1 - S$ and Z using relationships in Gulland (1969:59). Observed estimates were compared against theoretical values calculated from the expression $\overline{Z}$ = 4.6/number of years in life span (Royce 1972:238). Typical maximum life span was approximated by the Beverton-Holt yield model parameter t_L (Gulland 1969), and typical maximum size was approximated as a corresponding length (l_L) following Alverson and Carney's (1975) definition that only 0.5-1% of the catch exceeds age t_L. Values of l_L were calculated from the cumulative length frequency for all fish captured in the period October 1977-August 1981. We calculated specific values of t_L from l_L by solving for time in von Bertalanffy (Gulland 1969:40) and quadratic regression equations. Total mortality rates and growth data presented are termed *apparent* because they may be affected by emigration as noted; if so, they overestimate mortality but underestimate sizes at age.

Ovaries were prepared to estimate fecundity (FEC) using procedures similar to Bagenal (1957) and Simpson (1959). Entire ovaries of 60 Early Developing, Late Developing, Gravid, or Ripe fish were removed, split, everted, placed in Gilson's solution for 1-3 mo, and agitated using a magnetic stirrer to enhance separation of ova from connective tissue. Connective tissue was removed and supernatant siphoned off until only ova remained. Eggs were then placed in a beaker, filled to 200 ml with water, and magnetically stirred to be uniformly dispersed. Fecundity was determined for each fish by taking a 2 ml sample from each of three fixed levels in the beaker (at 25, 100, 175 ml) to enumerate eggs. Samples were pooled to calculate a mean/2 ml for each fish because, although significant, differences in mean egg count per level over all fish were small (627, 592, and 598, respectively; n = 60 for each level). Mean counts/2 ml were expanded to determine fecundity as the number of eggs in the total water volume.

Regression relationships were calculated following standard procedures (Helwig and Council 1979; Snedecor and Cochran 1980). Von Bertalanffy growth was calculated using Fabens' (1965) program. All length measurements presented herein are total length unless stated otherwise, and all length frequencies are moving averages of three. Conversions between standard length and total length used regressions presented herein.

We use the verb "recruit" and the noun "recruitment" herein to describe areas in which young *L. fasciatus* descend to the bottom from their pelagic (Johnson 1978) early stages. This usage conforms to Beverton and Holt's (1957) meaning of recruitment, because these bottom areas are exploited, and to Ricker's (1975) meaning, because fish also then enter the exploited phase of life.

RESULTS

Maturation and Spawning Periodicity

Larimus fasciatus from the northwestern Gulf mature at 80-130 mm as they approach age I. Gonad development was distinct at 80-150 mm when most females entered the Early Developing stage (Fig. 4). All fish in Late Developing and later stages were >130 mm. These data are supported by regressions of ovary weight on length (Fig. 2) in which extrapolated x-intercepts were 75-125 mm during the April-October period when spawning occurs. Age compositions and sizes presented later indicate *L. fasciatus* mature to first spawn at 12-14 mo.

Little somatic growth seemingly occurs after *L. fasciatus* enter late stages of gonad development. Mean lengths of fish were 146 mm in the Late Developing stage, 147 mm when Gravid, 149 mm when Ripe and Spawning/Spent, and 150 mm when Resting (Fig. 4). Maximum and minimum sizes also remained constant through these stages.

Larimus fasciatus spawn within a broad period from April through November. Fish in Ripe or Gravid stages occurred throughout this period (Fig. 5), slopes and elevations of regressions of ovary weight on length generally were highest (Fig. 2), and GSI maximums usually were high (Fig. 3). Gonad analyses are supported by 1) recurrent collections of fish 20-40 mm from November through February each year in the period 1978-81 which probably were 1-3 mo old and indicate spawning from September through November (Fig. 6), and 2) collections of distinct groups of fish 40-80 mm in the period mid-June through August in 1980 and 1981 which probably were 3-5 mo old and indicate spawning from April through June.

Little or no spawning of *L. fasciatus* occurs from

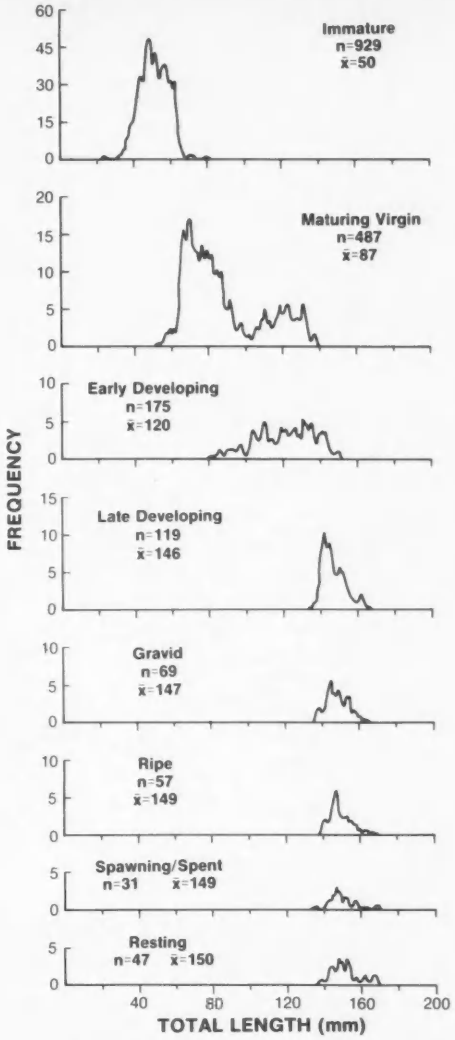

FIGURE 4.—Length frequencies of immature and female *Larimus fasciatus* by gonad maturity stage. See Table 1 for maturity stage criteria.

December through March. Almost all fish were in the Immature, Maturing Virgin, Early Developing, or Resting stages in that period (Fig. 5). Few were in the Late Developing stage then and none were Gravid or Ripe. In addition, mean and maximum GSI values were lowest during the December-March period (Fig. 3) as were the slopes and elevations of regressions of ovary weight on length (Fig. 2). Gonad analyses are supported by the absence of fish 20-80 mm from late February to mid-June each year (Fig. 6) with the exception of fall-spawned fish whose growth in late winter and spring is clearly followed.

Although *L. fasciatus* spawn within a broad time period, spawning primarily occurs during what we interpret as two discrete periods, a major fall period (September-November) and a very minor spring period (April-June). Mean and/or maximum GSI values were highest in the periods May-June and September-November, and these peaks were separated by troughs in the periods July-August and December-April (Fig. 3). Although few fish were Ripe in August, nearly all were in Late Developing, Gravid, Ripe, and Spawning/Spent stages from September through November (Fig. 5); few were in Immature, Maturing Virgin, or Early Developing stages then. Fall-spawned fish greatly predominated each year and formed length-frequency modes easily followed through the spring and summer after their recruitment in fall and winter (Fig. 6). A minor spring spawn is indicated by distinct, but not abundant, groups of fish 40-80 mm in the periods August 1980 and June-August 1981 (Fig. 6) and by the occurrence of a few (14) Gravid and Ripe stage fish from April through June and Late Developing fish in March (Fig. 5). No recently recruited spring-spawned fish were evident after August (Fig. 6), but they may be represented by the few intermediate-sized fish from an unclear spawned group in January and March 1980 and February 1981.

Little or no spawning of *L. fasciatus* occurs in July and August. No fish 20-40 mm (1-3 mo old) were captured from July through October (Fig. 6). Only two fish were Gravid or Ripe during July and August and few were in the Late Developing stage then (Fig. 5).

Calculated hatching dates agree with the major fall-spawning period—September-November—indicated by gonad and length-frequency analyses. Depending on data points included, calculated hatching dates were 27 July or 15 October 1978, 17 September 1979, and 27 August or 17 October 1980 (Table 4). Hatching dates of 15 October and 17 October seem most realistic for 1978 and 1980. The earlier dates for those years are based on regressions fitted to all collections. The earliest two collections in those years, however, probably contribute upwardly biased size data

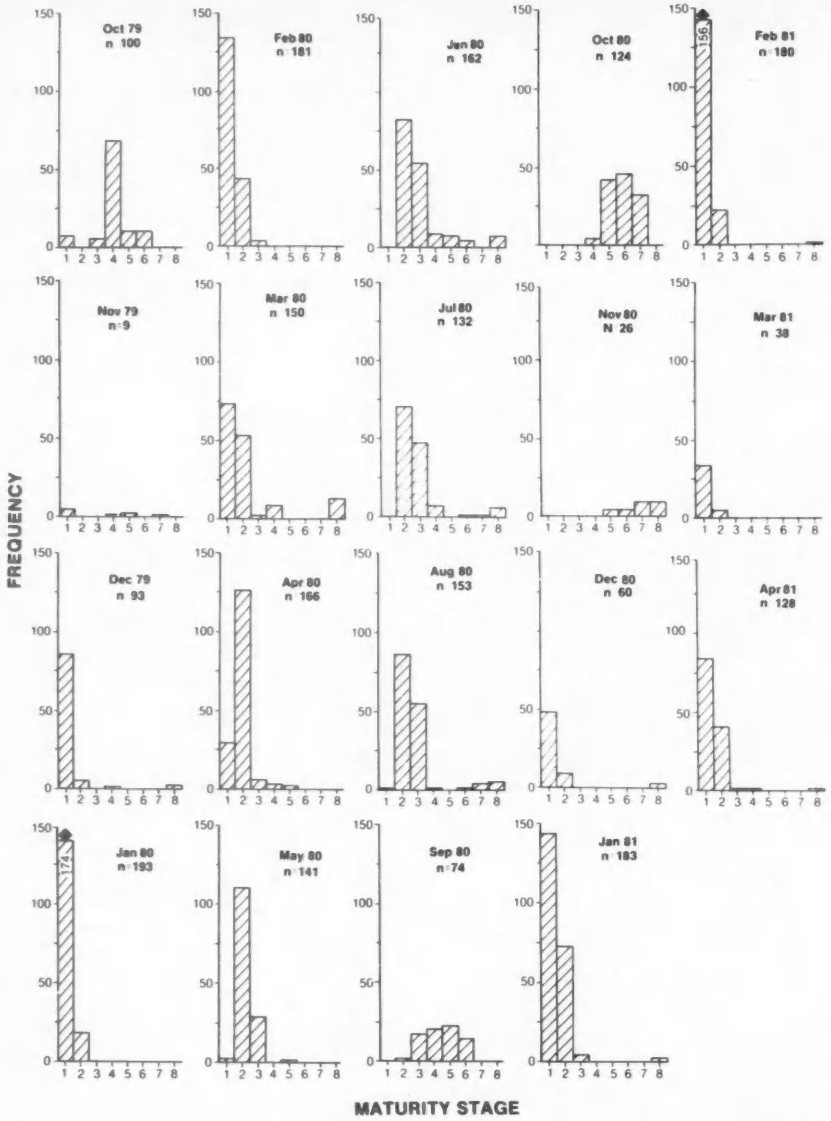

FIGURE 5.—Monthly gonad maturity stages of immature and female *Larimus fasciatus*. Maturity stages (see Table 1) are 1 - Immature, 2 - Maturing Virgin, 3 - Early Developing, 4 - Late Developing, 5 - Gravid, 6 - Ripe, 7 - Spawning/Spent, and 8 - Resting.

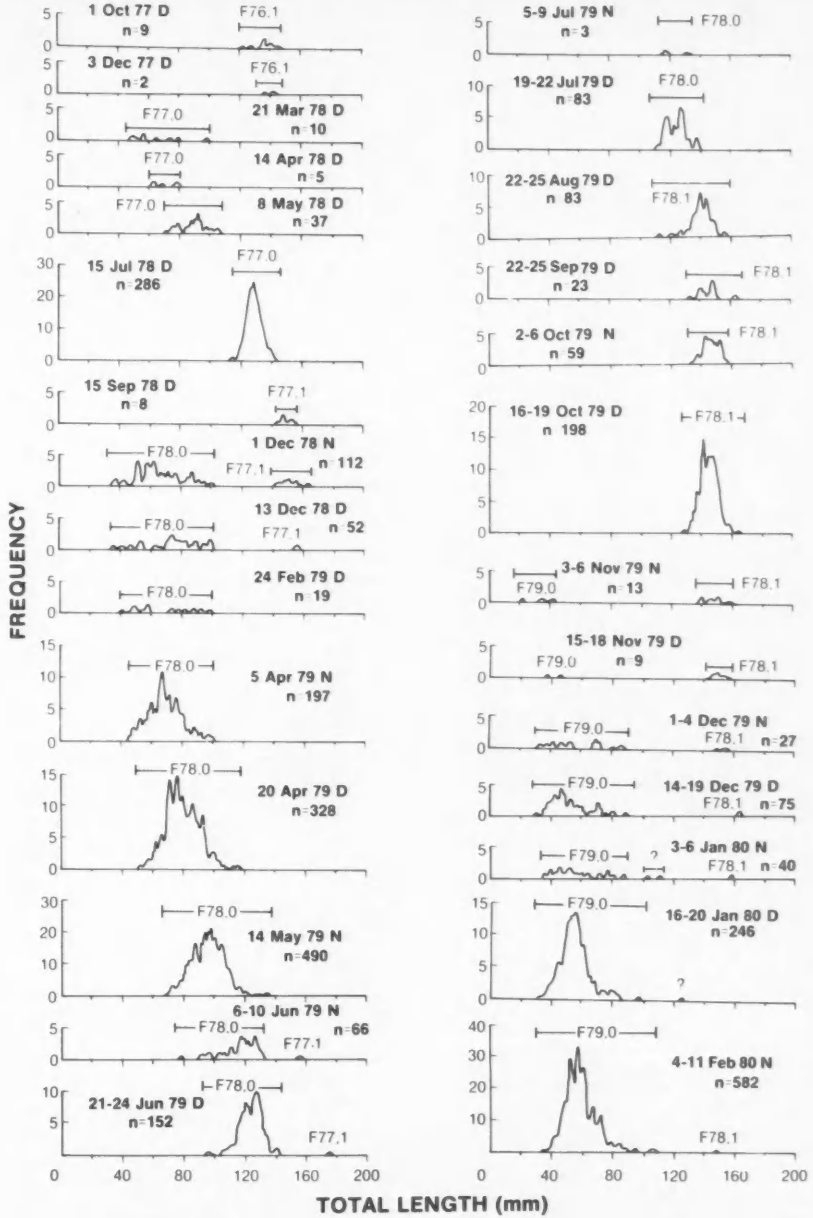

FIGURE 6.—Monthly length frequencies of *Larimus fasciatus* off Freeport, Tex. Day and night cruises are indicated by D and N. Bars in each panel depict size range of indicated spawned group; further detail is in Table 3. The letter and first two digits within a bar indicate spawned groups; the last digit is age in years, e.g., F77, 1

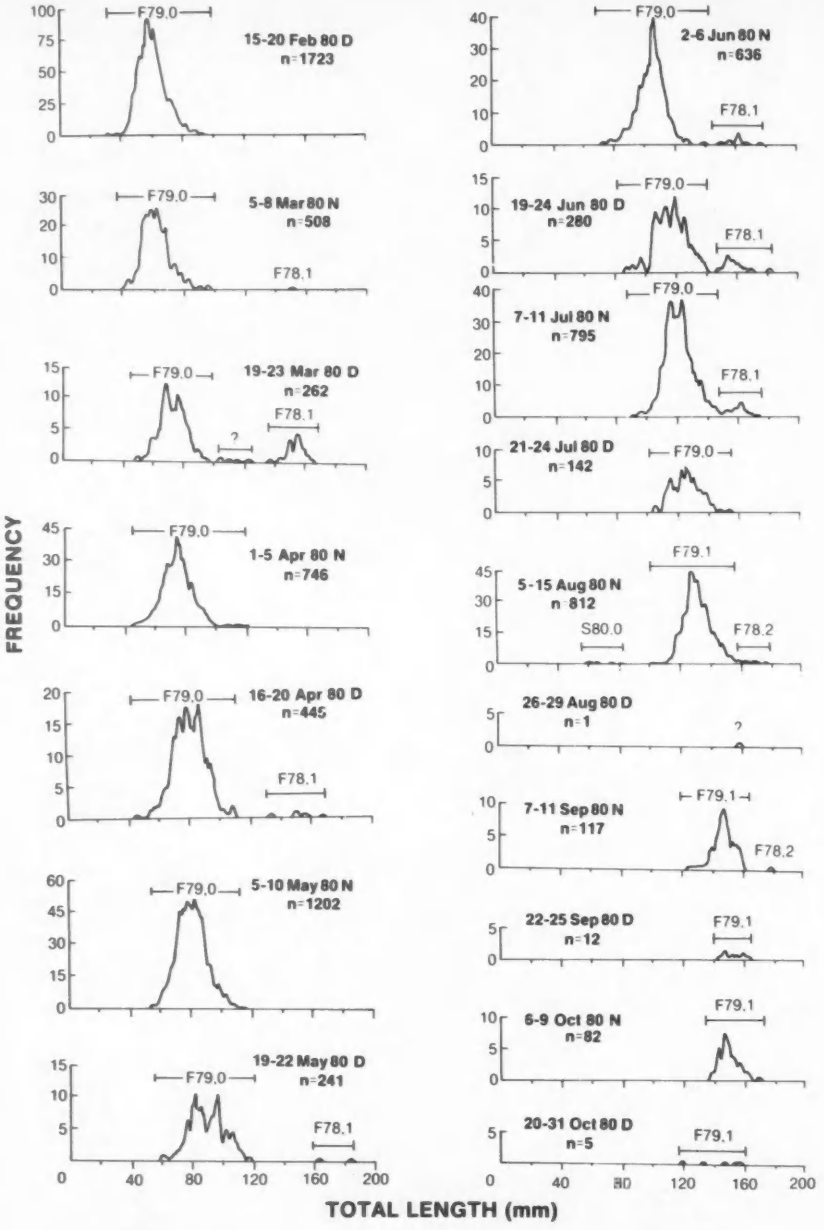

FIGURE 6.—*Continued*—represents the fall 1977-spawned group when age I. Age designation for each cohort changed in August to simplify reference between Figures 6 and 10 D; true ages in August only approach those indicated.

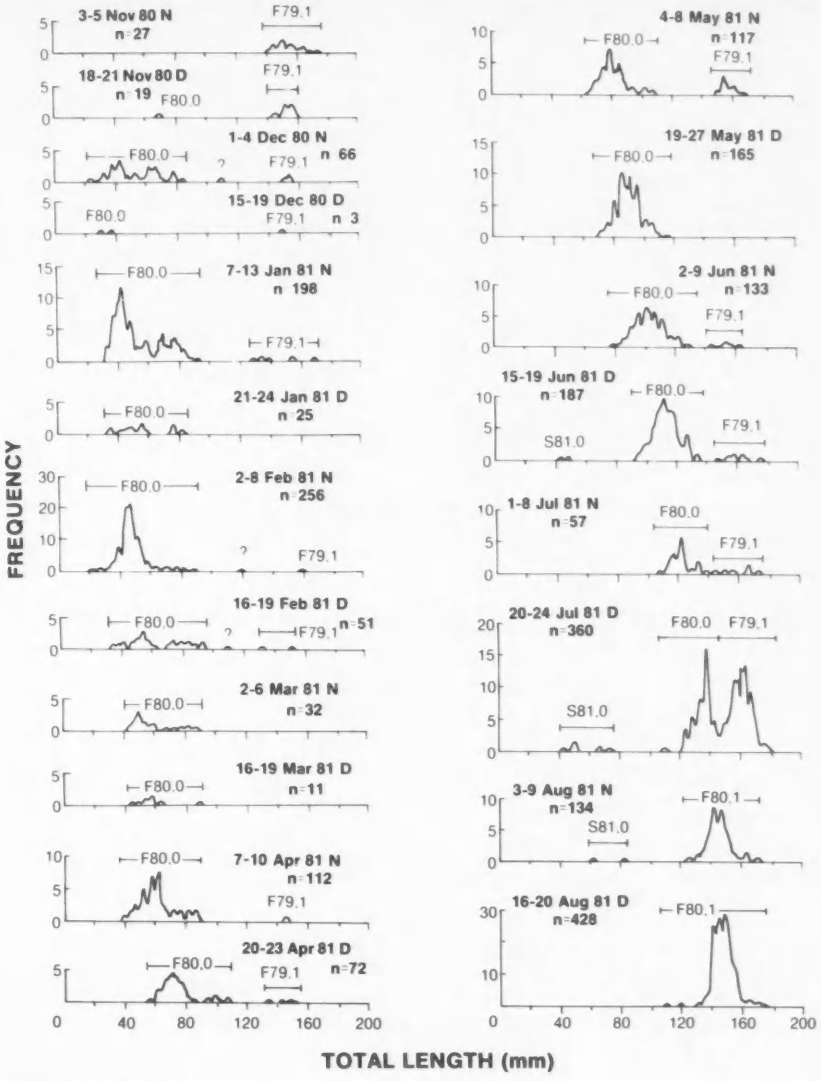

FIGURE 6.—*Continued.*

that reflect gear selection for large fish or incomplete recruitment of smaller fish; mean sizes in those collections were as large as or larger than means in subsequent collections and seem to be outliers (Fig. 7A, C). Coefficients of determination were higher when the earliest two collections were excluded (Fig. 7A, C).

The period of successful spawning spans 60-90 d within the major September through November interval. Based on mean 99% confidence limits for observations and growth per day in each April-June period, calculated durations of fall spawning periods were 76 d in 1977, 76 in 1978, 87 in 1979, and 64 in 1980 (Table 2). These estimates fall within and agree with the broad 90-d duration of the fall-spawning period indicated by gonad maturity and weight data.

The predominant fall-spawned groups are produced by fish that first spawn when 12-14 mo old and the minor spring-spawned groups by fish 19-21 mo old. Fall-spawned fish apparently do not spawn when 5-7 mo old in their first spring, because GSI values for fall 1979 and fall 1980 fish remained low during their initial springs (Fig. 8B, C). Peaks in GSI values from September through November in 1979 and 1980 were formed by fall 1978 and fall 1979 fish, first spawning at 12-14 mo of age (Fig. 8A, B). Peaks in GSI values from April through June in 1980 and 1981 were formed by fall 1978 and fall 1979 fish that spawned when 19-21 mo old (Fig. 8A, B). We were not able to determine age when spring-spawned groups spawn, because these fish were clearly identifiable only until 3-5 mo old (see section on Age Determination and Growth).

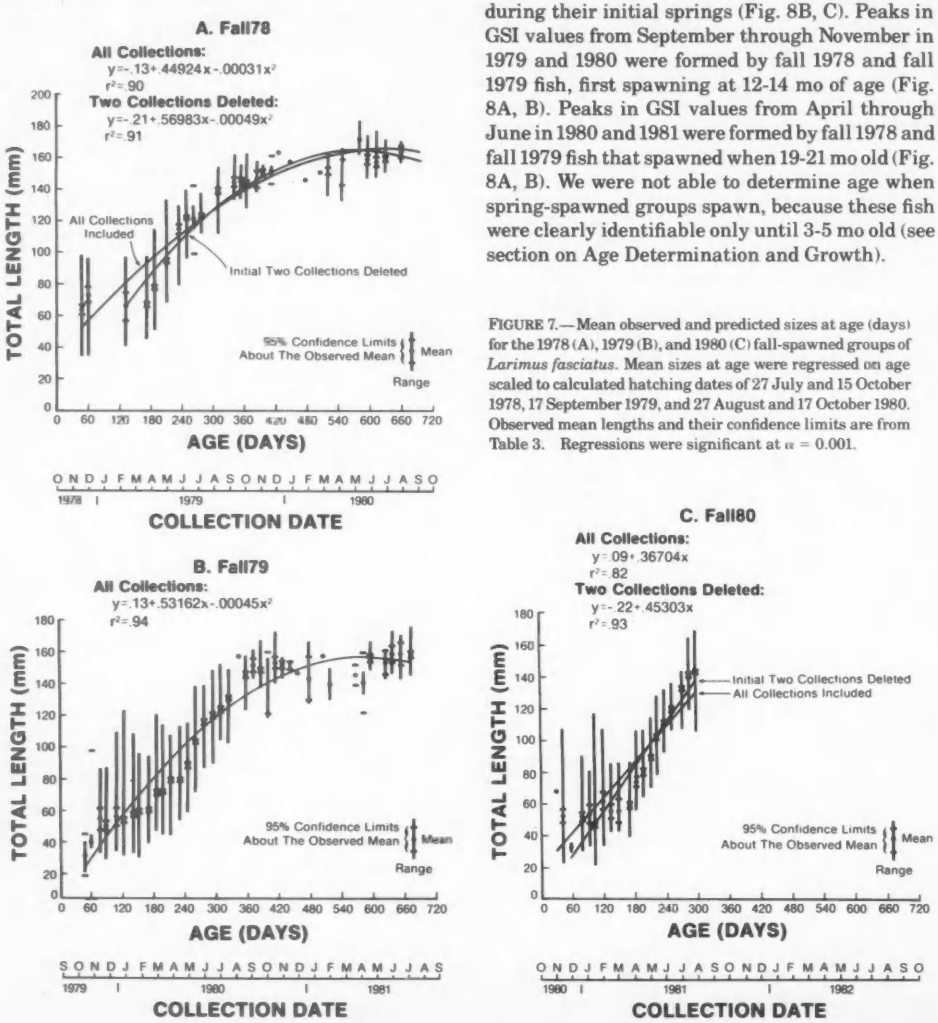

FIGURE 7.—Mean observed and predicted sizes at age (days) for the 1978 (A), 1979 (B), and 1980 (C) fall-spawned groups of *Larimus fasciatus*. Mean sizes at age were regressed on age scaled to calculated hatching dates of 27 July and 15 October 1978, 17 September 1979, and 27 August and 17 October 1980. Observed mean lengths and their confidence limits are from Table 3. Regressions were significant at $\alpha = 0.001$.

Bathymetric Distribution, Recruitment, and Movements

The bathymetric distribution of *L. fasciatus* in the northwestern Gulf off Freeport extends from <5 to 55 m. This species was most abundant at 5 m, the shallowest depth occupied (Fig. 9). Abundance declined sharply between 5 and 18 m and remained low from 18 to 36 m. Only one specimen was collected deeper than 36 m.

Young-of-the-year *L. fasciatus* in the northwestern Gulf recruit in waters <5-16 m when 2-4 mo old. Fall-spawned young 30-100 mm recruited almost exclusively in 5-16 m from November through April (Fig. 10A, B). Only four young-of-the-year specimens at 18-22 m were collected deeper than 16 m. Similarly, spring-spawned young 60-80 mm recruited only at 5-16 m in the period August-October (Fig. 10D).

Greatest recruitment of fall-spawned *L. fasciatus* occurred in the shallowest depths sampled. Recent fall-spawned recruits were most abundant by far at 5 m in November-April (Fig. 10A, B). Abundance then sharply declined with depth and was very low deeper than 16 m in that period.

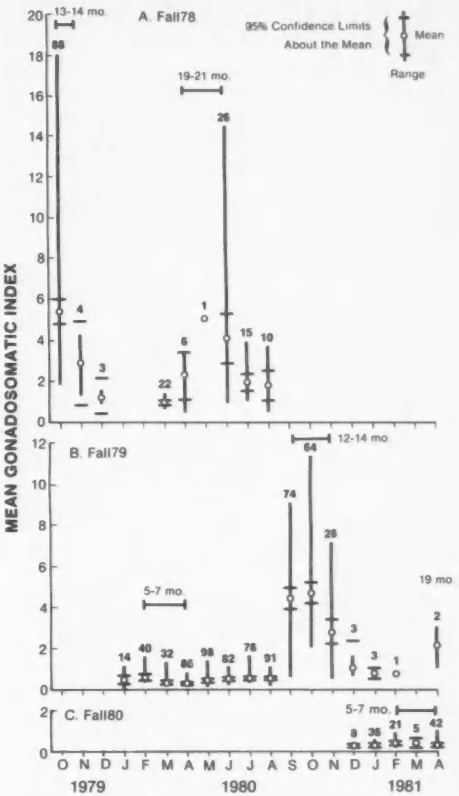

FIGURE 8.—Monthly mean gonadosomatic indices, sample sizes, ranges, and 95% confidence limits about means for the 1978 (A), 1979 (B), and 1980 (C) fall-spawned groups of *Larimus fasciatus*. Age in months is indicated for each spring and fall spawning period.

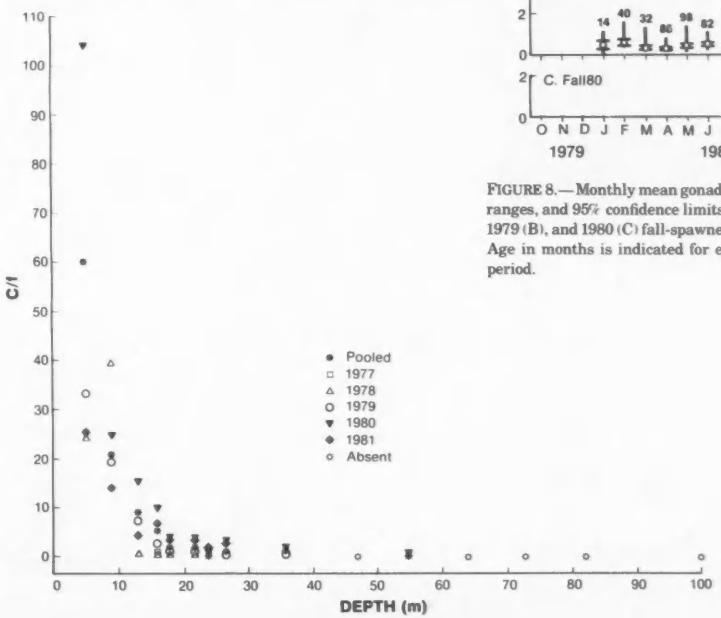

FIGURE 9.—Catch/effort (mean number of individuals per 10 min tow) by depth for *Larimus fasciatus* off Freeport, Tex., each year and pooled, October 1977-August 1981.

Fall-spawned *L. fasciatus* gradually disperse toward deeper water in late spring or summer. The distribution of young-of-the-year in May-July was similar to that in November-April (Fig. 10C). Fish approaching age I showed a clear offshore shift in distribution by August-October when abundance greatly declined at 5-13 m, became highest at 16-22 m, and was as high at 24-27 m as at 5-13 m (Fig. 10D). Fish approaching age I became distributed to 36 m, a depth they previously did not occupy, in August-October.

Larger *L. fasciatus* lead the offshore dispersal as they approach age I. Size compositions of the young-of-the-year were uniform with depth in November-April (Fig. 10A, B). They became skewed toward the right in May-July and show a gradient of increasing size with depth in August-October which suggests larger, presumably older, fish move offshore first.

Adult fall-spawned *L. fasciatus* in the northwestern Gulf occupy the 13-24 m bathymetric range from November through April while

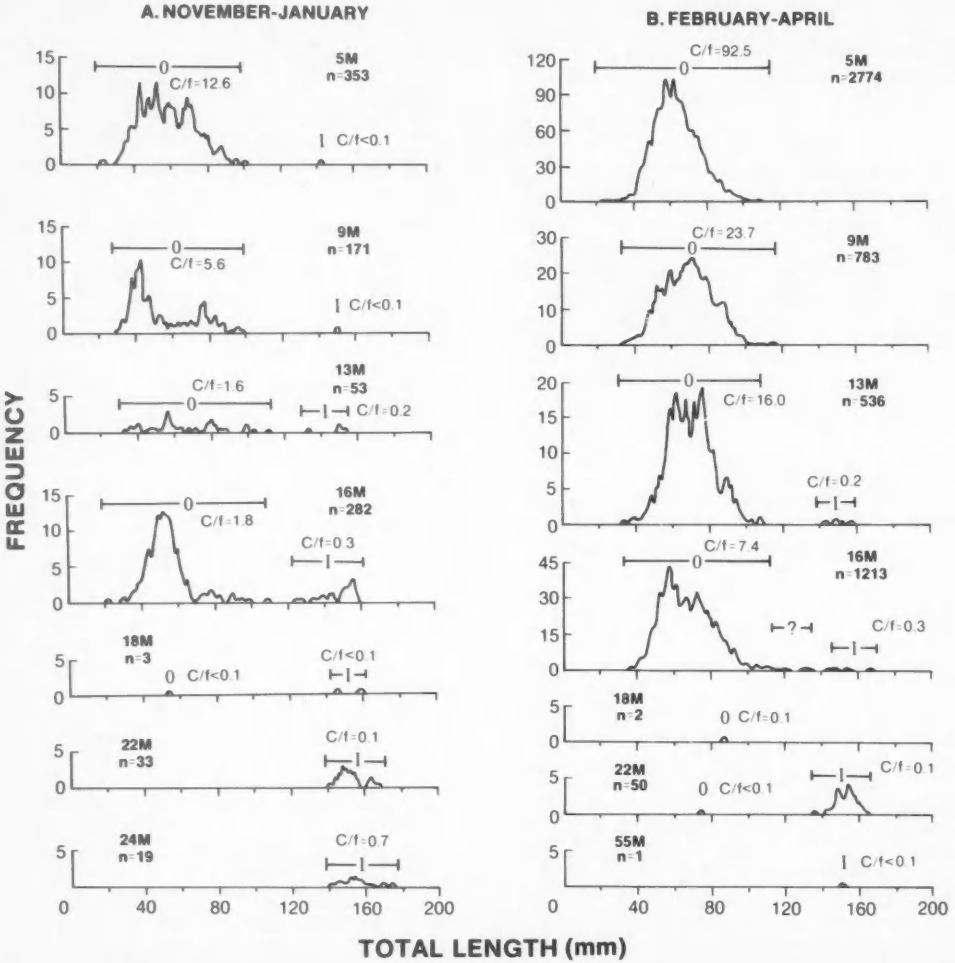

FIGURE 10.—Length frequencies and catch per effort (mean number of individuals per 10 min tow) by depth for *Larimus fasciatus* off Freeport, Tex.: A) November-January, B) February-April, C) May-July, and D) August-October. Data in each panel were pooled over the

young-of-the-year recruit inshore. Newly age I and older fish were most abundant at 13-24 m in November-April (Fig. 10A, B). Few were captured at 5-9 m then.

Age Determination and Growth

Few spawned groups of *L. fasciatus* exist at any one time in the northwestern Gulf and only one normally predominates. No more than three spawned groups were present at any time (Fig. 6). This maximum occurred only in August 1980 and June-July 1981 when spring-spawned fish recruited to join two fall-spawned groups. These were the only occasions when spring-spawned fish were clearly identifiable and their abundance was

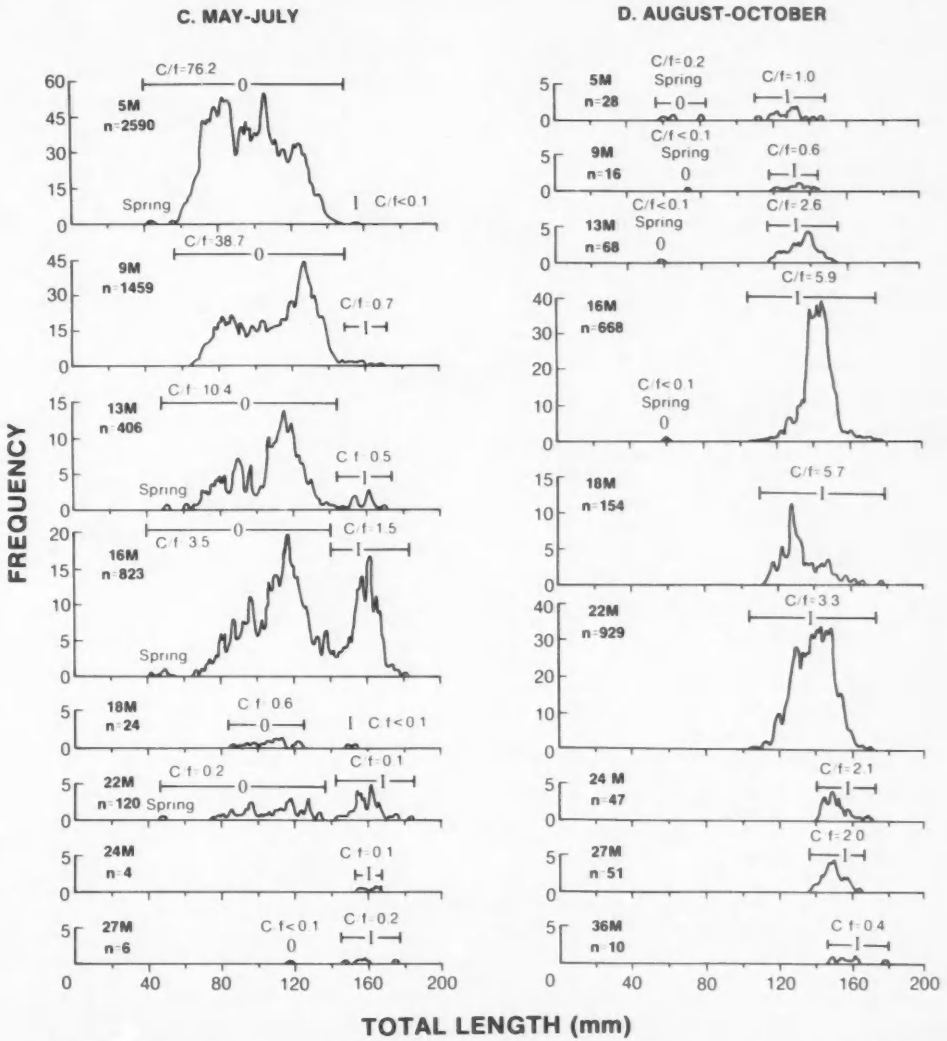

FIGURE 10.—*Continued*—period October 1977-August 1981 because length frequencies were similar each year. Designated ages are for fall-spawned fish except where noted. Age design· ·n for each cohort changed in August.

negligible even then. Although two fall-spawned groups, represented by young-of-the-year and age I fish, often were captured, only one predominated in any month except in July 1981 when fish approaching age II were abundant but disappeared thereafter. Once fully recruited, each fall-spawned group predominated to age I and then nearly disappeared as the next fall group began to recruit.

Larimus fasciatus is not abundant after 12 mo of age in the northwestern Gulf and reaches only 21-23 mo there. Fall-spawned fish were abundant after 12 mo of age (Fig. 6) only in July 1981 when they approached age II. Fall-spawned groups disappeared at 15-23 mo of age (Table 5, Fig. 6). The few spring-spawned fish captured were identifiable only until 3-5 mo of age (Table 5, Fig. 6). Fish of intermediate size between clearly defined fall-spawned groups in January and March 1980 and February 1981 could have been spring-spawned, but their identity is not clear.

Slightly larger *L. fasciatus* occur in the north central Gulf than in the northwestern area. Maximum and mean sizes were greater in the north central Gulf (max. = 187 mm, $\bar{x}$ = 160 mm) than in the northwestern area (max. = 173, $\bar{x}$ = 146) during the period October and November, ignoring the seven recently hatched recruits captured in the latter area (Fig. 11).

Only one or two spawned groups of *L. fasciatus* apparently predominate in the north central Gulf, probably fish that became age I and age II in the fall. We are not able to confidently identify modal groups to assign ages and, particularly, delineate sizes where age groups overlap in that area (Fig. 11), because we made only one cruise there, not the time-intensive series that permits confident age designations for the northwestern Gulf. Analyses such as linear transformation of cumulative percentage frequencies using probability paper (Harding 1949), moreover, do not and cannot resolve this situation because of the original problem: the underlying length frequency is not absolutely clear. However, the 48 mm range of sizes (139-187 mm) for fish in the north central Gulf is only slightly larger than a 35 mm range (130-165 mm) that tightly brackets most fish in the northwestern Gulf where only one fall group predominated (Fig. 11). Moreover, sizes in the north central Gulf in the period October-November were only slightly larger than and greatly overlap those for northwestern Gulf fish which were just age I. These facts suggest only one or at most two spawned groups predominated in the north central Gulf, fish just age I and age II. This interpretation is supported by our findings noted later that 1) the largest fish we captured in the northwestern Gulf (182 mm) was only 20 mo old, 2) von Bertalanffy predictions indicated mean sizes of 164 and 181 mm at age II in the northwestern Gulf depending upon variation between fall-spawned groups, and 3) the observed size range was 143-176

TABLE 5.—Periods of time, sizes, and age when spawned groups of *Larimus fasciatus* were last captured.

Spawned group	Period last captured	Size (mm TL)	Age (mo)	Comments
Fall 1976	Early December 1977	136-141	15-16	Very few ever captured.
Fall 1977	Late June 1979	174	21-22	Few ever captured.
Fall 1978	Early September 1980	177	22-23	Few captured after October 1979.
Fall 1979	Mid-July 1981	146-176	22-23	Few captured after October 1980, except for late July 1981.
Spring 1980	Early August 1980	58-80	3-4	Collected only in August 1980.
Fall 1980	Mid-August 1981	105-170	10-11	Still dominant in last collection.
Spring 1981	Early August 1981	58-79	3-4	Very few ever collected.

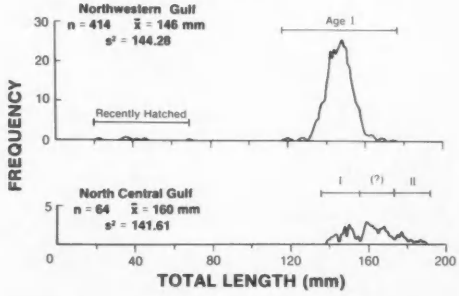

FIGURE 11.—Length frequencies and age designations for all *Larimus fasciatus* captured in the period October-November in the northwestern (1977-80) and north central (1982) Gulf of Mexico. Means, n, and s^2 ignore seven recent recruits (<70 mm) in the northwestern Gulf.

mm in July for the abundant fall 1979-spawned group as it approached age II in the northwestern Gulf. We have assumed fish in the north central Gulf were produced in the major fall-spawning period, not the minor spring one, and that differences in size compositions do not reflect only possible intra-Gulf differences and greater size at age in the north central Gulf. Comprehensive collections in that area are needed to resolve the latter assumption.

Apparent growth of *L. fasciatus* in the northwestern Gulf was similar between fall-spawned groups, mean sizes being 130-150 mm at age I and 155-180 mm at or approaching age II. Observed mean sizes and ranges at age I, based on pooled data from September and October (Table 3), were 134 mm (120-143) for fall 1976 fish, 148 mm (145-152) for fall 1977 fish, 145 mm (127-164) for fall 1978 fish, and 147 mm (118-168) for fall 1979 fish. These sizes at age I agree with quadratic regression predictions of 142 and 134 mm (Fig. 7) and von Bertalanffy model predictions of 137 and 131 mm for fall 1978 and fall 1979 fish, respectively. Observed mean size and ranges at or approaching age II (Table 3) was 159 mm (150-172) in July 1980 for fall 1978 fish, 159 mm (143-176) in July 1981 for fall 1979 fish, and 164 mm (156-177) in August-September 1980 for fall 1978 fish. These values are only slightly larger than a quadratic regression prediction of 155 mm at age II for fall 1978 fish (Fig. 7A), and are the same as or a little smaller than von Bertalanffy model predictions of 164 and 181 mm at age II for fall 1979 and fall 1978 fish, respectively.

Fitted von Bertalanffy equations based on hatching dates of 15 October for fall 1978 fish and 17 September for fall 1979 fish were

$$\text{Fall 1978: } l_t = 201\,(1 - e^{-0.003162(t-1.574)})$$

$$\text{Fall 1979: } l_t = 176\,(1 - e^{-0.003670(t+4.696)})$$

where l_t = length in millimeters, and t = time in days. Annual K values were 1.15 and 1.34, respectively. Respective annual t_0 values (0.00431 and −0.01287) were small which may reflect our forcing the curve through the origin.

Apparent growth of fall-spawned *L. fasciatus* follows an S-shaped intrayear pattern and is greatest in the spring and summer. Observed mean sizes at age showed a clearly S-shaped pattern (Fig. 7). Adjusted growth increments were small early in life (Fig. 12) and may reflect cool-water temperatures then, gear selection for larger young, or a pattern of incomplete recruitment in which smaller, younger fish gradually recruit to join early recruits that are slightly larger and older. Growth increments for age 0 fish were greatest in March-June, peaking in early June (26.7 and 32.1 mm/30 d). Growth increments decreased as maturation occurred from July through September, became small after spawning in October-January, and increased slightly in June-August as the fish approached age II.

Apparent sizes of *L. fasciatus* at or approaching age I in the northwestern Gulf reached a plateau in August-September and for many months later. Mean sizes of fish at or approaching age I remained constant then, and 99% confidence limits for observations generally remained uniform at 130-160 mm (Table 3, Fig. 6). This pattern suggests an exodus of larger individuals and/or cessation of growth coincident with gonad maturation (see section on Maturation and Spawning Periodicity).

Maximum Size, Life Span, and Mortality

The maximum size *L. fasciatus* reach in the northwestern Gulf is about 180 mm, but more typically individuals reach only 160-165 mm. The largest of the 13,676 fish we collected there was 182 mm; 99% were <161 mm and 99.5% were <164 mm (Fig. 13), these sizes being estimates of l_L.

Typical maximum life span of *L. fasciatus* appears to be only 1-2 yr in the northwestern Gulf. A value of t_L = 1-2 yr is reasonable for that area because 1) fish average 155-180 mm at or approaching age II and 130-150 mm at age I with the upper 99% confidence limits for observations at age I generally being 160-165 mm (Table 3), 2) l_L values of 161 and 164 mm predict t_L values of 1.3-2.0 yr (Table 6), 3) the largest specimen was 20 mo old when collected in May 1980, and 4) *L. fasciatus* disappeared off Texas at 15-23 mo of age (Table 5),

TABLE 6.—Values of t_L (yr) for *Larimus fasciatus* calculated from l_L (mm TL) using quadratic and von Bertalanffy equations scaled to hatching dates of 15 October for fall 1978 and 17 September for fall 1979 fish. The apex of the parabola for fall 1979 fish was 157 mm so that t_L values could not be calculated for that cohort.

Spawned group	l_L	t_L calculated from: Quadratic regression	von Bertalanffy equation
Fall 1978	161	1.33	1.40
Fall 1978	164	1.44	1.47
Fall 1979	161	—	1.83
Fall 1979	164	—	1.99

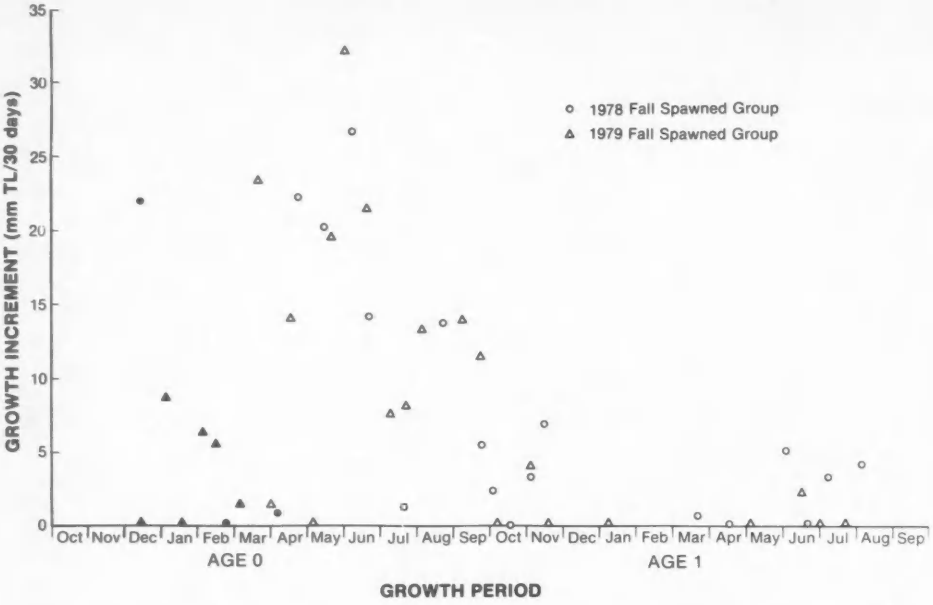

FIGURE 12.—Monthly growth increments for 1978 and 1979 fall-spawned *Larimus fasciatus*. Unadjusted growth increments (Table 3) were converted to growth/30 d, omitting collections of five or less fish. Negative growth is rounded to zero. Values denoted by darkened symbols may reflect incomplete recruitment, gear selection for larger young, or cool-water temperatures early in life.

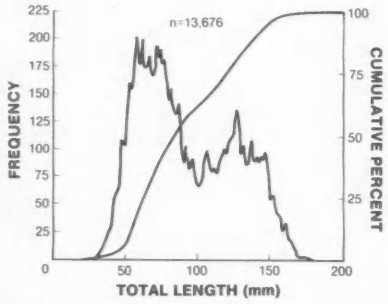

FIGURE 13.—Length frequencies and cumulative percentage of all *Larimus fasciatus* collected off Freeport, Tex., October 1977-August 1981.

and few ever approached age II except in July 1981 as previously noted. The latter instance suggests larger, older specimens of *L. fasciatus* may occur elsewhere; if so, our estimate of t_L may be too low for a stock that also ranges outside the northwestern Gulf.

Larimus fasciatus from fall-spawned groups have an *apparent* total annual mortality rate of 90-100% in the northwestern Gulf, mean time and cohort-specific values being 92-100%. Time-specific values of $1 - S$ were 100% in 17 of the 38 mo in which fish were collected (Fig. 6) because only one fall-spawned group was present and N_t was zero in the ratio N_t/N_0. Time-specific mortality estimates for the 18 remaining months gave ratios whose percentage values ranged from 89.93 to 99.96%; 14 exceeded 94%. Pooled estimates using Heincke's procedure were 97.18-100% depending on the spawned groups compared (Table 7). By pooling the Heincke numerators and denominators from each comparison an average time-specific $1 - S$ was 98.24%, or 96.86% if data from July 1981 are included. Cohort-specific values of $1 - S$ were 100% in 12 of the 24 mo for fall 1978 fish and in 2 of the 12 mo for fall 1979 fish because N_t was zero. Cohort-specific estimates for the remaining 6 mo in the fall 1978 cohort ranged from 97.83 to 99.81% except in June and July 1980 when estimates were 64.84 and 55.05%. Estimates for the remaining 7 mo in fall 1979 cohort ranged

TABLE 7.—Pooled time-specific and cohort-specific mortality estimates for *Larimus fasciatus* using Heincke's procedure (Ricker 1975). Symbols represent: N_0, youngest spawned group in Heincke's estimate; S, annual survival rate; $1 - S$, annual mortality rate; and Z, instantaneous mortality rate.

N_0	S	$1 - S$	Z
Time-specific			
Fall 1977	0	1.0000	∞
Fall 1978	0.0083	0.9917	4.79
Fall 1979	0.0180	0.9820	4.02
Fall 1980	0.0282	0.9718	3.57
Heincke's Pooled	0.0176	0.9824	4.04
Cohort-specific			
Fall 1978	0.0810	0.9190	2.51
Fall 1979	0.0317	0.9683	3.45

from 94.44 to 99.84% except in July 1981 when it was 74.43%. The low estimates in June and July reflect the unusual instance previously noted of immigration by fish approaching age II. Pooled cohort-specific estimates of $1 - S$ using Heincke's procedure were 91.90% for fall 1978 fish and 96.83% for fall 1979 fish (Table 7).

Sex Ratio and Fecundity

Male and female *L. fasciatus* appear equally abundant. The observed sex ratio of 1.00 males to 1.02 females among 2,502 mature or maturing fish examined in the period October 1979-April 1981 did not differ significantly from 1:1 ($\chi^2 = 0.19$; df = 1; $\alpha = 0.05$).

Mean fecundity of *L. fasciatus* in Gravid and Ripe stages was 70,453 eggs. Observed fecundity ranged from 32,333 to 143,800 eggs/female. Untransformed and log-log transformed linear regressions of fecundity on total length and total weight and related statistics are presented in Table 8; the former regression is depicted in Figure 14. The untransformed regression is a better fit ($100r^2$ being 29.7 vs. 27.1 for length and 35.1 vs. 28.4 for weight), but the transformed regression permits extrapolation over a broader size range. Fecundity statistics were based only on Gravid and Ripe fish, because residual plots for untransformed data indicated a relationship between fecundity and maturity stage (Fig. 15): maximum fecundity occurred in the Gravid and Ripe stages.

Weight, Girth, and Length Relationships

Total weight-total length, girth-total length, and standard length-total length regressions are presented in Table 8 with related statistics. Total length-total weight regressions for males and females were not significantly different in slope ($F = 0.35$, df = 1, 1936, $\alpha = 0.05$) or in elevation ($F = 1.62$, df = 1, 1936, $\alpha = 0.05$) so one pooled equation is presented for them. Total length-total weight regressions for males and females pooled and for immatures, males, and females pooled were significantly different in slope ($F = 44.87$, df = 1, 4808, $\alpha = 0.05$), but one equation that pools all sizes may be useful and is presented. Calculated slopes significantly exceeded $\beta = 3.0$ at $\alpha = 0.05$ for both length-weight relationships (males and females pooled, $t = 53.06$; immatures, males, and females pooled, $t = 60.41$).

DISCUSSION

Spawning Periodicity

We found that the broad April to November period within which *L. fasciatus* spawns generally agrees with many studies, including Hildebrand and Cable (1934), Miller (1965), Christmas and Waller (1973), and Ross (1978). However, our interpretation is new that little or no spawning oc-

TABLE 8.—Fecundity, total weight-total length, girth-total length, and standard length-total length regressions for *Larimus fasciatus* with supporting statistics. All regressions were significant at $\alpha = 0.01$; r is from Ricker's (1973) GM regression. Measures are grams and millimeters. See Methods for symbols.

Equation	n	TL range	$100r^2$	Residual MS	Corrected total SSx	Corrected total SSy	$\bar{x}$	$\bar{y}$	GM r
FEC = −295,307 + 2,498.36 TL	40	136-163	29.7	4.966×10^5	1,280.00	2.686×10^7	146.4	70,453	4,581.2
$\log_{10}$FEC = −5.5049 + 4.7689 $\log_{10}$TL	40	136-163	27.1	0.0178	0.0111	0.9280	2.17	4.82	9.1573
FEC = −32,999 + 2,223.57 TW	40	136-163	35.1	4.588×10^5	1,906.00	2.686×10^7	46.5	70,453	3,753.7
$\log_{10}$FEC = 2.6564 + 1.3013 $\log_{10}$TW	40	136-163	28.4	0.0175	0.1554	0.9280	1.67	4.82	2.4435
$\log_{10}$ TW = −5.5981 + 3.3481 $\log_{10}$ TL (males + females)	1,938	52-179	99.3	0.0015	34.42	388.67	2.03	1.20	3.3605
$\log_{10}$ TW = −5.4761 + 3.2883 $\log_{10}$ TL (males + females + immatures)	2,874	22-179	99.4	0.0025	108.91	1,184.74	1.92	0.84	3.2983
G = −1.21 + 0.77 TL	2,871	22-179	99.2	7.75	2,628,914 (G)		92.09	69.35	0.77
TL = 2.35 + 1.29 G	2,871	22-179	99.2	13.09	4,439,633 (TL)		69.35	92.09	1.30
SL = −5.63 + 0.83 TL	2,875	22-179	99.8	2.23	3,066,599 (SL)		92.08	70.76	0.83
TL = 6.96 + 1.20 SL	2,875	22-179	99.8	3.24	4,446,964 (TL)		70.76	92.08	1.20

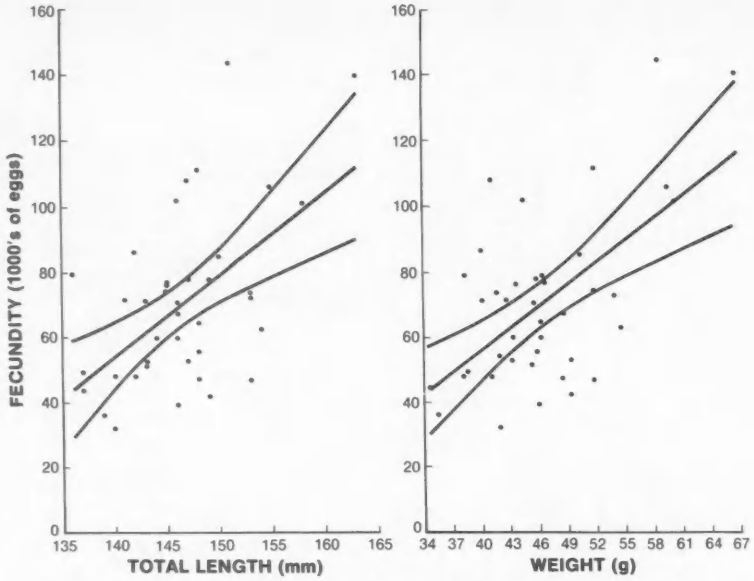

FIGURE 14.—Regressions of fecundity on total length and total weight with 95% confidence limits for $\bar{y}_x$ for *Larimus fasciatus*.

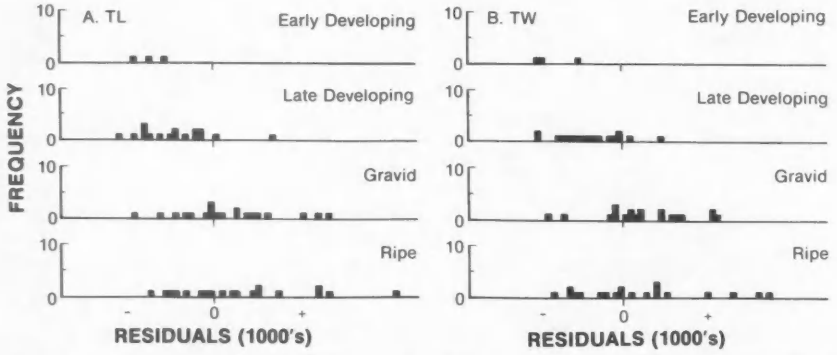

FIGURE 15.—Residual plots of maturity stages of *Larimus fasciatus* for relationship between fecundity and total length (A) and total weight (B) regressions.

curs in July and August and that spawning primarily occurs in two discrete periods, a major fall peak in September-November and a minor spring peak in April-June. The existence of distinct spring and fall spawning periods is supported by 1) Hoese's (1965) collection of larval fish only in June (11.5-25 mm SL modal length) and October (14-39 mm SL modal length) off Port Aransas, Tex., 2) Ross's (1978) collection off North Carolina of presumably fall-spawned fish in February (79 mm modal TL = 60 mm SL) and what must be spring-spawned fish in July (75 mm modal TL = 57 mm SL), 3) Powles's (1980) collections of larval fish in the periods April-May and August-September but not in June-July between Cape Canaveral and Cape Fear, and 4) collections of

larval fish in the periods April-June and August-October between Cape Lookout and Chesapeake Bay (Berrien pers. commun. footnote 7 in Powles 1980). This bimodal pattern, moreover, is similar to findings of distinct spring- and fall-spawning periods in other Gulf fishes such as *Cynoscion arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), and *Peprilus burti* (Murphy 1981). Murphy and Chittenden[7] integrated biological findings with hydrographic data of Kelly and Randall[8] and suggested hydrographic reasons for this pattern in *P. burti* and *C. nothus*, which probably apply also to *L. fasciatus* and many other species: spawning is timed to coincide with the periodicity of downcoast alongshore currents (toward Mexico) and onshore Ekman transport at the surface. These phenomena probably transport pelagic eggs and larvae inshore and "downstream" to nurseries in the northwestern Gulf from spawning grounds located "upstream" in or toward the north central Gulf. Current transport mechanisms reverse in the summer (a variable period but about mid-June-early August) and would carry pelagic eggs and larvae offshore, which presumably is unfavorable to survival in many species, or toward the north central Gulf. If spawning is substantial, and successful, during summer, our length-frequency data and those for the other species cited indicate summer-spawned individuals do not subsequently appear in the northwestern Gulf. Presumably, their existence would be reflected as unimodal, or at least not clearly bimodal, length frequencies when adequate data become available for the north central Gulf.

Our finding that the few spring-spawned fish disappeared after August at 3-5 mo of age agrees with Hildebrand and Cable (1934) who collected what must have been spring-spawned fish in July ($\bar{x}$ = 34 mm, range 3-70 mm ?L) and August ($\bar{x}$ = 54 mm, range 3-77 mm ?L) off North Carolina and noted they were absent later. Because the magnitude of spring spawning appears so small, for practical stock assessment purposes, our data could just as well be interpreted as one long period with little or no spawning from April to August. It seems more meaningful, however, to regard the spawning of *L. fasciatus* as occurring during two discrete periods because Murphy and Chittenden (footnote 7) suggested a hydrographic basis for that pattern.

Our findings are new that fall-spawned groups spawn in both spring and fall periods and that spring spawning is the product of fish about 20 mo old. Shlossman and Chittenden (1981) noted that temporal isolation of spawned groups in *C. arenarius* implied reproductive isolation and might indicate separate populations. The temporally separate spawned groups in *L. fasciatus*, however, are not reproductively isolated and apparently do not form separate populations because the same spawned group spawns in both periods. This simplifies management, because separate data may not be necessary for both spawning periods, especially considering that one is very small.

Shlossman and Chittenden (1981) and DeVries and Chittenden (1982) noted that the existence of two spawned groups in *C. arenarius* and *C. nothus* might buffer population stability as a multiple year class structure does in longer lived species. In *L. fasciatus*, however, the contribution that spring-spawned groups make to total population size is probably too small to buffer fluctuations at any reasonably "normal" stock size.

Bathymetric Distribution

Larimus fasciatus primarily is restricted to the inner continental shelf. Our finding, that they range from <5 to 55 m but are most common from 5 to 16 m, agrees with Hildebrand (1954), Miller (1965), Burns (1970), Milstein and Thomas (1976), and Wenner et al. (1979a, b). Franks et al. (1972) captured most specimens in 37-55 m off Mississippi which supports Chittenden and McEachran's (1976) suggestion that the white shrimp community, of which *L. fasciatus* is a member, penetrates into deeper water in the north central Gulf than it does in the northwestern area. However, Springer and Bullis (1956) collected fish at 106 m off both Mississippi and Texas.

Age Determination and Growth

Little literature exists on age determination and growth in *L. fasciatus*. We determined age by length-frequency analysis because our data came from a long-term set of cruises close enough together in time that modes were easily followed.

[7]Murphy, M. D., and M. E. Chittenden, Jr. Unpubl. manuscr. Reproduction, movements, and population dynamics of the gulf butterfish, *Peprilus burti*. 66 p. Marine Research Laboratory, Florida Department of Natural Resources, 100 Eighth Avenue, S.E., St. Petersburg, FL 33701.

[8]Kelley, F. J., Jr., and R. E. Randall. 1980. Physical oceanography. *In* R. W. Hann, Jr. and R. E. Randall (editors), Evaluation of brine disposal from the Bryan Mound .te of the Strategic Petroleum Reserve Program, p. (1-1)-(1-93). National Technical Information Service, Springfield, VA 22150 (DOE/P010114-1).

Moreover, we observed so little overlap of lengths from different spawned groups that few individuals could have been incorrectly aged and basic conclusions on apparent growth and mortality would be little affected by such error. As Geoghegan and Chittenden (1982) found for *Stenotomus caprinus*, length-frequency analysis can be a superior method to age *L. fasciatus* because 1) little spawning occurs in other than one major discrete period each year, 2) length frequencies within spawned groups are reasonably described by a normal distribution, 3) growth of large and small fish within a spawned group appears uniform since the variance was generally constant between cruises, and 4) life span is short so age determination need be applied only to a few ages, the ideal situation for using length frequencies (Lagler 1956; Tesch 1971). Ross (1978) successfully used scales and otoliths to determine age of North Carolina fish, but we were not able to do so in limited trials and did not pursue these methods further because it seemed unnecessary.

Larimus fasciatus reach slightly larger sizes at age off North Carolina than apparent sizes we found in the northwestern Gulf. Von Bertalanffy predictions of size at age off North Carolina (Ross 1978) were 153 mm (121.3 mm SL) at age I, 188 mm (151.1 mm SL) at age II, and 209 mm (168.0 mm SL) at age III compared with quadratic and von Bertalanffy predictions of 130-150 mm at age I and 155-180 mm at or approaching age II for the northwestern Gulf. Our finding that growth is greatest in the spring and summer agrees with Ross (1978).

Maximum Size, Life Span, and Mortality

The largest *L. fasciatus* we found in the northwestern Gulf (182 mm) is smaller than most maximum sizes reported from the north central Gulf (Louisiana: 208 mm by Hildebrand 1954, 195 mm ?L by Dunham 1972, and Mississippi: 202 mm by Franks et al. 1972, 189 mm by Christmas and Waller 1973, 187 mm in our data), and much smaller than those reported from the Atlantic coast of the United States (New York to Florida: 220 mm by Wilk and Silverman 1976, Chesapeake Bay: 215 mm ?L by Hildebrand and Schroeder 1928, off North Carolina: 205 mm ?L by Hildebrand and Schroeder 1928, 206 mm ?L by Hildebrand and Cable 1934, and 225 mm = 182 mm SL by Ross 1978). The largest record is a 271 mm specimen collected off Mississippi (Franks 1970). The larger size off the Atlantic coast of the United States may reflect greater longevity there, especially from about Cape Lookout or Cape Hatteras north where zoogeographic change in population dynamics may occur (White and Chittenden 1977). Ross (1978) collected age III fish off North Carolina, but the oldest fish we collected only approached age II.

The appearance of larger *L. fasciatus* in the north central Gulf than in the northwestern area follows a pattern apparent in a variety of species (Murphy and Chittenden footnote 7) including *C. nothus, P. burti, S. caprinus, Brevoortia patronus*, and *Micropogonias undulatus*. These authors suggested this could reflect 1) small but fundamental percentage composition and population dynamics differences between these areas, 2) greater biomass at all ages in the north central Gulf, not necessarily population dynamics differences, so that greater numbers of large fish might be captured there even if percentage compositions did not vary, and/or 3) probable permanent emigration from the northwestern to the north central Gulf by larger, older, spawning or postspawning fish as they approach age I. They suggested the last explanation applied to *C. nothus, P. burti*, and probably other fishes, and that it would be manifested as between area population dynamics differences. The following findings also suggest that *L. fasciatus* too more or less permanently emigrates from the northwestern to the north central Gulf as spawning and age I approaches 1) the plateaus in length formed in August and seeming cessation of somatic growth in later stages of gonad development, and 2) the appearance in the northwestern Gulf in July 1981 of an abundant fall-spawned group approaching age II. This older spawned group, and parallel spawned groups in other years, was absent or rare in all other months even though our data were based on 71 cruises and 3,390 tows over 4 yr.

Because larger, older *L. fasciatus* probably emigrate to the north central Gulf, the typical maximum life span of 1-2 yr we observed for the northwestern area may be a little low for a stock that ranges over both areas. With the exception of the very large specimen that Franks (1970) found, the largest individuals reported from the north central Gulf are only 189-208 mm as noted. This is not much larger than our largest specimen (182 mm) from the northwestern area, which was 20 mo old. Moreover, these maximums are similar to von Bertalanffy predictions of mean sizes at age II (165-185 mm) or at age III (175-195 mm) that we found, and sizes of 188 and 204 mm Ross (1978)

found at ages II and III, respectively. Therefore, a t_L value of 2-3 yr may be realistic for a stock that ranges over the north central and northwestern Gulf. We assume in suggesting this, that differences in size compositions do not reflect only possible intra-Gulf growth differences and greater size at age in the north central Gulf.

The mean *apparent* time-specific and cohort-specific total annual mortality rates we observed for the northwestern Gulf (92-100%) agree with theoretical estimates (Royce 1972:238) of 90-100% if maximum life span typically is only 1-2 yr as we found for that area. Because larger, older *L. fasciatus* probably emigrate to the north central Gulf, our observed mortality estimates are probably too high for a stock that ranges over both areas. Theoretical values of 80-90% based on a 2-3 yr typical maximum life span may be more realistic, a magnitude which agrees with the lowest values tenable for other sympatric species such as *C. arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), *S. caprinus* (Geoghegan and Chittenden 1982), and *P. burti* (Murphy 1981). Even values of 80-90% are higher than the three lowest mortality rates we found for the northwestern Gulf (55-74%) and rates of 57 and 81% that Ross (1978) reported off North Carolina; the latter range of values is theoretically appropriate as an average over life spans of 3-5 yr, although present data suggest 4-5 yr is too large a value of t_L for the Gulf.

General

Population dynamics of *L. fasciatus* are similar to those reported from the northwestern Gulf for *M. undulatus* (White and Chittenden 1977), *C. arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), *S. caprinus* (Geoghegan and Chittenden 1982), *P. burti* (Murphy 1981; Murphy and Chittenden footnote 7), and in *Centropristis philadelphica* ignoring its hermaphroditism (Ross and Chittenden[9]). Our findings support the suggestions that 1) groundfishes of the white and brown shrimp communities in the Gulf have evolved a common pattern of population dynamics characterized by small size, early age at maturity, short life spans, high mortality rates, and rapid turnover of biomass (Chittenden and McEachran 1976; Chittenden 1977), and 2) more or less permanent spawning or post-spawning emigration may occur from the northwestern Gulf to the north central area as fish approach age I (Murphy and Chittenden footnote 7). Because typical maximum life spans may be closer to 2-3 yr than 1-2 yr, these fishes may be a little more sensitive to growth overfishing than Chittenden's (1977) simulations, based on a 2 yr life span, suggest for *M. undulatus*.

[9]Ross, J. L., and M. E. Chittenden, Jr. Unpubl. manuscr. Reproduction, movements, and population dynamics of the rock sea bass, *Centropristis philadelphica*, in the northwestern Gulf of Mexico. 50 p. North Carolina Division of Marine Fisheries, North Carolina Marine Resources Center, Manteo, NC 27954.

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IMPLICATIONS OF INVESTING UNDER DIFFERENT ECONOMIC CONDITIONS ON THE PROFITABILITY OF GULF OF MEXICO SHRIMP VESSELS OPERATING OUT OF TEXAS[1]

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ABSTRACT

Due to the inflationary trend in recent years coupled with fluctuating shrimp prices, the shrimp business has become a highly uncertain undertaking. The financial performance of a sample of the Gulf of Mexico shrimping fleet, operating out of the Texas coast, was examined over a 10-year period (1971-80). The results indicate that investments made in the early part of the 1970's performed better than those made in the latter part. Periods of low inflationary levels appeared to be more favorable to investments in the shrimp fishery than periods of high inflationary levels.

In terms of economic profits, steel vessels generally did better than wooden ones. Medium-sized vessels (18.6-20.0 m in overall length) were the most efficient vessels to operate in the Gulf of Mexico.

The Gulf of Mexico supplies a major share of the shrimp landed by commercial shrimp producers in the United States. From 1977 to 1981, Gulf shrimp landings accounted for 62% of the U.S. total. In 1981, 161 million kg of commercial shrimp valued at $463.4 million are landed in the United States. The Gulf of Mexico accounted for 76% of these landings and 87% of the value. Although the Gulf shrimp fishery is the most valuable in the United States, individual harvesters within the industry are not without their financial problems.

Of late, the high variability in shrimp landings and prices has created short-run uncertainty among shrimp producers (Caillouet and Patella 1978; Warren and Griffin 1980). Coupled with this, operating costs have been significantly increasing over the years, to the extent that, it has become quite difficult for fishermen to stay in business (Griffin et al. 1978).

There have been several costs and returns and/or investment analyses conducted on fishing vessels in recent years (Gates and D'Eugenio 1975; Noetzel 1977; Jones et al. 1979; Roberts and Saas 1979; Prochaska and Cato 1981); however, none have been concerned with the effect of inflation on investing in a fishing vessel. This paper uses the period 1971-80 to draw conclusions about the effect of low, medium, and high inflationary periods on return to investment. The study further examines the implication of unstable shrimp prices and rising costs of operations on the profitability of the shrimp industry in the Gulf of Mexico. Finally, the performance of wooden and steel hulled vessels in various size classes is compared.

METHODS

Data Description

The data used in this study are an accumulation of 5 yr of data collection, which have been reported in previous publications (U.S. Department of Commerce 1971-1980, 1971-1981; Griffin et al. 1974, 1976; Griffin and Nichols 1976; Warren and Griffin 1978). Although data were collected for other Gulf states, only data for vessels operating out of Texas are used in this study, since it is the only state for which data were available for all 5 yr that data were collected.

In the original studies, data were collected by personal interview in ports from Galveston to Port Isabel for 1971, 1973, 1974, 1975, and 1977 and estimated for the remaining years. Additional information was obtained from officials of various lending institutions which engage in shrimp vessel financing, from boat builders, and from the National Marine Fisheries Service.

Cost

The variable cost items for which data were gathered included ice, fuel, nets, supplies, repairs

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and maintenance, crew shares, payroll taxes, and packing charges. Fuel consumption by vessel class, for which primary data were unavailable, was estimated according to the following relationship:

$$Y_i = \frac{\Sigma\left(X_{ij} N_{ij}\right)}{\Sigma N_{ij}}$$

where Y_i = estimated number of gallons (1 gal = 3.79 l) used per year by vessel class i.
X_{ij} = actual number of gallons (1 gal = 3.79 l) used in year j by vessel class i.
N_{ij} = number of vessels in vessel class i in year j.

The nets, supplies, and repairs and maintenance variables were similarly adjusted like Y_i to account for unequal numbers of vessels in the sampling years. These variables were deflated into real terms, using the industrial price index, and the weighted average was determined. From the weighted average of the 5 yr for which data were available, adjusted nominal values were determined for the other years. Crew shares were estimated at 33% of value of catch. Packing charge was set at $0.10 per pound (0.454 kg) of shrimp landings.

Fixed costs include insurance, depreciation, interest, and opportunity cost. Reported data were used to determine fixed charges for overhead items, while charges relating directly to investment—depreciation, insurance, and interest—were calculated in nominal dollars for new vessels. Overhead values for years that data were not available were calculated using the industrial price index in the same manner as with variable cost.

Insurance charges were set at 4% of new vessel cost. The standard straight-line formula was used to determine depreciation. In this study the terminal value of the vessel was calculated in two ways: 1) at 100% of original cost, and 2) at salvage value at the end of 1980. The market rates, which prevailed over the years, were employed in deriving the cost and returns budget.

Revenue

Catch relationships were estimated for years for which no data were available by utilizing the following formulation:

$$EC_{ij} = WC_i\,(TL/TL_j)$$

where $WC_i = \dfrac{\sum_j N_{ij} \cdot RC_{ij}}{\sum_j N_{ij}}$ and

$RC_{ij} = AC_{ij}/(TL_i/TL)$.
EC_{ij} = estimated catch by vessel class i for year j where j = 1971, 1972, ..., 1980.
TL_j = Texas landings for year j, = 1971, 1972, ..., 1980.
TL = average Texas landings for the 1971-80 period.
RC_{ij} = real catch of vessel class i in year j for the 5 yr vessel data were available.
AC_{ij} = actual catch of vessel class i for year j for the 5 yr vessel data were available.
N_{ij} = number of vessels of class i for year j for the 5 yr vessel data were available.

Exvessel[3] prices per pound of shrimp were adjusted according to the formula given below using the average value from the National Marine Fisheries Service data for Texas and that from the survey to generate exvessel prices for those 5 yr that data were not collected.

$$AP_{ij} = (A_i - B) + TP_j$$

where AP_{ij} = adjusted exvessel price per pound (0.454 kg) of shrimp for vessel i in year j.
TP_j = Texas prices as reported by the National Marine Fisheries Service for year j, where j = 1971, ..., 1980.
AI = average exvessel price per pound (0.454 kg) of shrimp for vessel i over the 5 yr data were available.
B = average exvessel price per pound (0.454 kg) of shrimp

[3]It is recognized that exvessel price of shrimp is greatly influenced by seasonal fluctuation in local supply as well as the size composition of catch (Caillouet and Patella 1981). However, this study implicitly accounts for such trends by employing primary data collected for 1971, 1973, 1974, 1975, and 1977. Therefore, the price represents a weighted average between the various shrimp sizes.

reported by the National Marine Fisheries Service.

Analyses

A computer program referred to as a budget generator was devised to organize and assimilate the data for various analyses. The program allowed data reports to be produced according to the desired vessel classifications, interest rate, percent financed, number of years financed, number of loan payments per year, depreciation method, crew share agreement, rate of packing charges, payroll tax rate, discount rate, and planning horizon. The program reported results in the form of annual costs and returns budgets and projected cash flow budgets.

The following analysis first examines a detailed annual income and cash flow statement for a vessel purchased new in 1971. This detailed annual income and cash flow is then compared for the same vessel operated under identical conditions, but purchased in 1977 and 1979. Next, six different types of vessels (three wood and three steel; Table 1) are compared by examining their net returns during the three different periods of investment. Finally, investment performance is analyzed through net present value (NPV).

In all the above analyses three investment periods (1971, 1977, 1979) are considered. A given vessel is assumed to be operated under identical conditions regardless of the investment period. Since the actual sale price of the vessel at the end of the investment period is determined by the economic environment at that time, a comparison is made between the effects of selling the vessel at a salvage value of 35 and 100% of the original price.

TABLE 1.—Number and types of Gulf of Mexico shrimp vessels surveyed operating out of Texas ports.

Vessel type[1]	1971	1973	1974	1975	1977
Wooden, 17.1-18.5 m	1	1	3	3	1
Wooden, 18.6-20.0 m	1	9	8	4	1
Wooden, 20.1-21.5 m	1	26	24	26	4
Steel, 18.6-20.0 m	0	14	19	21	17
Steel, 20.1-21.5 m	3	13	41	41	18
Steel 21.6-23.0 m	2	4	10	5	2

[1]Coast Guard registered length.

RESULTS

Detailed Annual Budgets and Cash Flow

Tables 2 and 3 represent detailed annual income and cash flow budgets for a newly financed 1971 steel vessel, 20.1-21.5 m in overall length. Over the 10-yr study period, annual revenue doubled although it decreased by 18.9% in 1974 and by 7.4% in 1980. The decrease could be attributed, in part, to the decrease in exvessel price for shrimp from \$4.23/kg to \$3.62 in 1974 and from \$8.38 to \$7.06 in 1980. Another contributing factor was poor landings recorded in those periods (Fig. 1).

TABLE 2.—Annual income statement for a steel vessel, 20.1-21.5 m. long, operating out of Texas ports, 1971 to 1980.

	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980[1]	1980[2]
Revenues	78,100	95,798	99,903	80,978	99,456	132,799	142,272	155,733	164,638	152,479	152,479
Variable costs											
Ice	1,502	2,062	2,052	1,656	1,903	2,169	2,859	4,371	4,002	4,105	4,105
Fuel	6,515	6,515	9,523	20,549	21,551	22,052	23,055	25,060	40,095	47,613	47,613
Nets, supplies, groceries	8,348	8,186	9,220	11,263	12,559	13,357	14,287	15,334	17,319	20,028	20,028
Repair and maintenance	5,563	5,455	6,144	7,505	8,369	8,901	9,521	10,219	11,541	13,347	13,347
Crew shares	25,773	31,613	32,968	26,723	32,834	43,824	46,950	51,392	54,331	50,318	50,318
Packing	2,580	2,899	2,440	2,679	3,003	3,178	3,891	3,586	2,873	3,143	3,143
Total	50,281	56,730	62,347	70,375	80,219	93,481	100,563	109,962	130,161	138,554	138,554
Fixed costs											
Depreciation	9,084	9,084	9,084	9,084	9,084	9,084	9,084	9,084	9,084	9,084	9,084
Insurance	5,191	5,191	5,191	5,191	5,191	5,191	5,191	5,191	5,191	5,191	5,191
Interest (vessel loan)[3]	6,910	6,412	5,879	5,308	4,697	4,042	3,340	2,589	1,785	923	923
Overhead	3,423	3,357	3,781	4,619	5,150	5,477	5,859	6,288	7,102	8,213	8,213
Total	24,608	24,044	23,935	24,202	24,122	23,794	23,474	23,152	23,162	23,411	23,411
Total operating costs	74,889	80,774	86,282	94,576	104,341	117,275	124,037	133,114	153,323	161,965	161,965
Net revenue	3,211	15,024	13,621	−13,599	−4,843	15,524	18,235	22,619	11,315	−9,487	−9,487
Net return after tax[4]	266	9,405	8,158	−17,106	−8,672	8,916	11,140	14,377	5,100	−15,383	45,273
Current equity	33,611	39,101	42,531	28,724	19,718	32,096	41,324	43,328	39,530	43,282	73,609
Required return to equity	3,946	4,391	4,636	3,326	2,686	4,250	4,992	5,273	5,190	5,376	9,142
Economic profit	−3,680	5,014	3,522	−20,433	−11,357	4,667	6,148	9,104	−90	−20,758	36,130

[1]Vessel sold for salvage value.
[2]Vessel sold for original purchase price.
[3]Vessel was purchased for \$129,767; 75% financed at 7.1% interest.
[4]The difference between net revenue and net return after taxes includes owner's salary, social security tax for owner, and income tax.

TABLE 3.—Annual cash flow statement for a steel vessel, 20.1-21.5 m. long, operating out of Texas ports, 1971 to 1980.

	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980[1]	1980[2]
Revenues											
Beginning cash balance	0	2,339	13,319	22,518	5,883	0	5,192	14,835	26,964	29,011	29,011
Receipt from shrimp	78,100	95,798	99,903	80,978	99,496	132,799	142,272	155,733	164,638	152,479	152,479
Capital receipts	0	0	0	0	0	0	0	0	0	38,930	129,767
Total cash inflow	78,100	98,137	113,222	103,496	105,381	132,799	147,463	170,568	191,602	220,420	311,257
Operating expenses											
Fuel	6,515	6,515	9,523	20,549	21,551	22,052	23,055	25,060	40,095	47,613	47,613
Other variable expenses	43,766	50,216	52,824	49,826	58,669	71,429	77,507	84,901	90,065	90,942	90,942
Fixed cash expenses	11,559	14,165	14,436	13,317	14,169	20,205	18,145	19,722	18,510	19,300	49,481
Total	61,840	70,896	76,783	83,692	94,389	113,686	118,707	129,683	148,670	157,855	188,036
Long- and short-term debt											
Long-term debt (principle)	7,011	7,509	8,042	8,613	9,224	9,879	10,581	11,332	12,136	12,998	12,998
Long-term debt (interest)	6,910	6,412	5,879	5,308	4,697	4,042	3,340	2,589	1,785	923	923
Total cash outflow	75,761	84,817	90,704	97,613	108,310	127,607	132,628	143,604	162,591	171,776	201,957
Cash situation											
Net cash balance	2,339	10,980	9,199	−16,635	−8,812	8,121	9,643	12,129	2,047	19,633	80,288
Cash available	2,339	13,320	22,518	5,883	−2,929	5,192	14,835	26,964	29,011	48,644	109,300
Ending cash balance	2,339	13,320	22,518	5,883	0	5,192	14,835	26,964	29,011	48,644	109,300
Net present value 0.1174										22,572	42,560

[1]Vessel sold for salvage value.
[2]Vessel sold for original price.

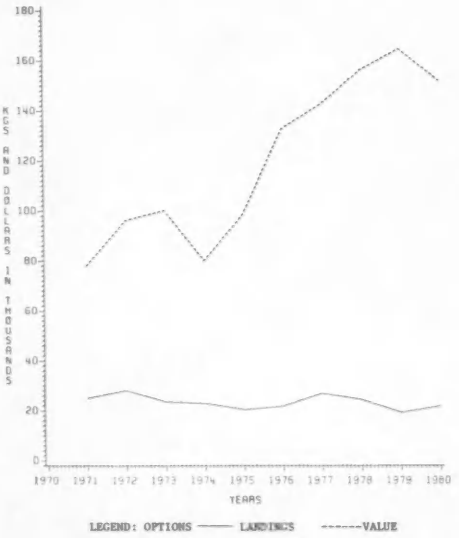

FIGURE 1.—Total Texas landings and value of landings for a typical steel vessel 20.1 to 21.5 m long by year.

There was no significant variation in total fixed costs during the 10 yr for two reasons: Depreciation and insurance charges were set at fixed levels, but while overhead charges increased gradually over the years, interest payments on vessel loans decreased by about the same margin. The highest total fixed cost incurred was $24,608 in 1971 and the lowest was $23,152 in 1978 (Table 2).

Total variable costs, on the other hand, increased by 175.5% over the 10-yr period. The highest increase of 18.4% occurred in 1979, and it was in direct response to an increase in fuel charges from $25,060 in 1978 to $40,095 in 1979 (Table 3). Expenditure on fuel showed a tremendous increase in 1974 by 115.7%; both of these increases were due to the sharp rise in fuel prices (Fig. 2).

In response to an increase in variable costs and relatively constant fixed costs, total operating

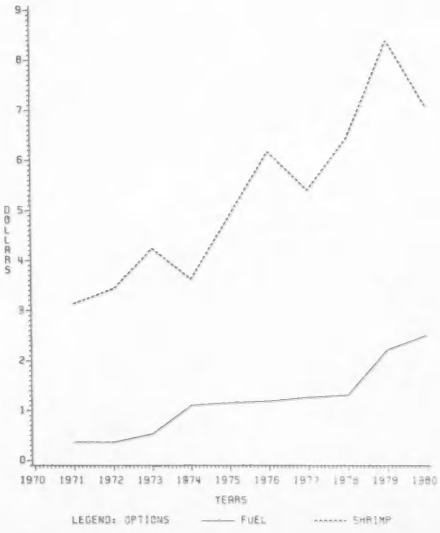

FIGURE 2.—Price of fuel and shrimp for a steel vessel 20.1 to 21.5 m long by year operating out of Texas ports.

costs more than doubled over the period 1971-80, from $74,889 to $161,965 (Table 2). The highest net revenue before taxes recorded was $22,619 in 1978. Losses were recorded in 1974, 1975, and 1980, and this could be due to the effects of inflation and poor harvest recorded in those years.

Terminal value has a critical effect on profitability. Decreased landings led to a substantial economic loss of $20,758 in 1980 (Table 2), when vessels were salvaged at 35% of their original values. Increasing the terminal value to 100% of cost resulted in a positive economic profit of $36,130, the highest obtained (Table 2). It was further observed that the net present value for the investment project increased by 72.5% when vessels were salvaged at their original costs rather than at the 35% level of their original values.

Investment in Different Time Periods

Tables 2 and 3 present the results of investing in a shrimp vessel in 1971. Considerable investment has been made in new shrimp vessels since 1977. Table 4 shows the annual increase and cash flow statements for purchasing the same steel vessel in 1977. Since the level of operations is held constant, revenue and variable costs are the same; fixed costs, however, changed dramatically.

In 1971, the value of the 20.1-21.5 m steel vessel was $129,767. In 1977, that same vessel cost $222,084, a 71.1% increase in price. The loan payment in 1971 was a little over $11,600/yr assuming a 10 yr note, but increased to $24,074/yr. If the vessel was purchased in 1971, profits were made in 1977 and 1978; for the vessel purchased in 1977, losses were incurred over the entire investment period. Losses were particularly substantial if the vessel was sold for salvage value at the end of 1980.

The cash flow statement shows that cash available was very low for 1977-79. There was about $35,000 difference in cash available in 1980, depending on whether the vessel had been sold for salvage value or for its original purchase price. For the vessel purchased in 1971, the net cash increase in 1977 was $9,643; and only $2,223 for the vessel purchased in 1977. In 1979 under the 1971 scenario, cash available would have increased $2,047; here it declined $6,252. Despite poor economic conditions, NPV was positive for both vessel sale prices, implying vessels would have had a greater return on investment than bonds purchased in 1977.

Table 5 shows the results of purchasing a vessel in 1979. The price of the vessel went up by about 26.8% since 1977, and substantial losses were incurred. The NPV is negative if the vessel is sold for its salvage value and positive if it is sold for 100% of its original purchase price. Short-term borrowing occurred when the vessel was purchased in 1979. In fact, the vessel owner had to borrow more than he was paying in principal on his original purchase note.

Economic Performance by Size and Construction

Figures 3 through 8 show variations in net revenue for the various vessel types used in the analysis. These variations follow a general pattern. For vessels purchased in 1971, net revenue peaked in 1972 and 1978 and dropped to minimum levels in 1974 and 1980. A major reason for this trend is that

TABLE 4.—Summarized annual income and cash flow statements for steel vessels, 20.1-21.5 m long, operating out of Texas ports, 1977 to 1980.

	1977	1978	1979	1980[1]	1980[2]
Income statement					
Value of landings	142,272	155,733	164,638	152,479	152,479
Total variable cost	100,562	109,961	130,160	138,555	138,555
Total fixed cost[3]	43,497	43,011	42,838	42,883	42,883
Net revenue	−1,787	2,761	−8,359	−28,959	−28,959
Economic profit[4]	−8,628	−5,006	−15,587	−43,663	−158
Cash flow statement					
Total cash inflow	142,272	157,956	172,165	313,654	375,838
Total cash outflow	140,049	150,429	170,890	180,396	187,041
Net cash balance	2,223	5,304	−6,252	131,983	187,522
Cash available	2,223	7,527	1,275	133,258	188,797
Net present value			-	12,759	47,954

[1]Salvage value set at 35% of original cost.
[2]Vessel sold for original purchase price.
[3]Vessel was purchased for $222,084; 75% financed at 7.93% interest.
[4]Economic profit is the net revenue adjusted for any changes in the value of operating inventories and capital items.

TABLE 5.—Summarized annual income and cash flow statements for steel vessels, 20.1-21.5 m long, operating out of Texas ports, 1979 to 1980.

	1979	1980[1]	1980[2]
Income statement			
Value of landings	164,638	152,479	152,479
Total variable cost	130,160	138,555	138,555
Total fixed cost[3]	61,449	63,668	63,668
Net revenue	−26,971	−49,745	−49,745
Economic profit[4]	−34,528	−68,559	−45,932
Cash flow statement			
Total cash inflow	164,638	383,999	421,689
Total cash outflow	184,132	215,631	218,132
Net cash balance	−19,493	187,861	223,049
Cash available	−19,493	168,368	203,556
Net present value		−9,355	18,140

[1]Vessel sold for salvage value.
[2]Vessel sold for original purchase price.
[3]Vessel was purchased for $269,210; 75% financed at 12.25% interest.
[4]Economic profit is the net revenue adjusted for any changes in the value of operating inventories and capital items.

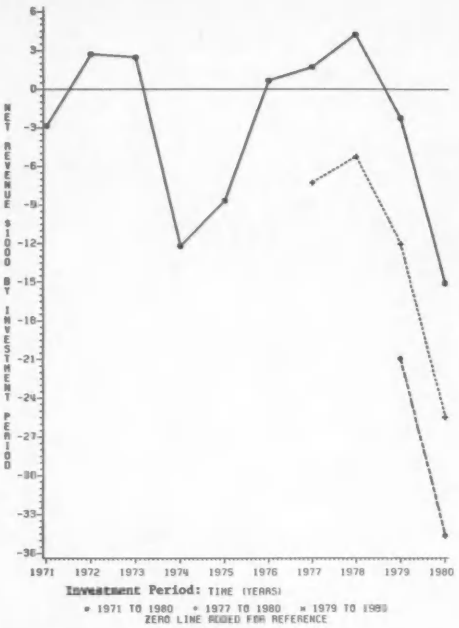
NET REVENUE $1000 BY INVESTMENT PERIOD
Investment Period: TIME (YEARS)
* 1971 TO 1980 + 1977 TO 1980 × 1979 TO 1980
ZERO LINE ADDED FOR REFERENCE

FIGURE 3.—Net revenue for a wooden vessel 17.1 to 18.5 m long operating out of Texas ports by investment period.

while tremendous increases in the value of landings were recorded in 1972 and 1978, 1974 and 1980 were the only periods in which the value of landings actually decreased. It can further be shown that fuel charges increased dramatically in 1974 and 1980 (Fig. 2), making those years particularly bad ones for Texas shrimp producers in terms of net revenue.

In general, steel vessels performed better economically than wooden vessels irrespective of the investment period. This may be attributed to the durability of steel vessels and their ability to operate under more adverse weather conditions than wooden vessels. The performance of 18.6-20.0 m steel vessels was particularly outstanding (Fig. 6) while the same size wooden types performed very poorly, recording losses throughout the study period (Fig. 4). As explained earlier, steel vessels are more durable and can spend more days offshore fishing than wooden vessels. Besides, steel vessels generally call for less maintenance and repair costs and attract a better quality crew than wooden ones. With the exception of the 17.1-18.5 and 18.6-20.0 m wooden vessels, which recorded losses over most of the period, all the other vessels performed satisfactorily.

Variation in Net Present Value

Evaluating the investments based on the net present value criterion, the 18.6-20.0 m steel vessels would be ranked as the best investments in the Gulf shrimp fishery (Table 6). Compared with the other vessel types, they consistently showed the highest net present values under all investment conditions examined. At the other end of the continuum lie the 18.6-20.0 m wooden vessels, which showed the poorest net present values under each investment condition, actually showing negative net present values and implying that investing in 18.6-20.0 m wooden vessels is not a feasible endeavor (Table 6).

With the exception of 18.6-20.0 m wooden vessels, 1971 investments showed the highest net present values, followed by those made in 1977. Investments made in 1979 were the least feasible; this may be attributed to unusually high capital

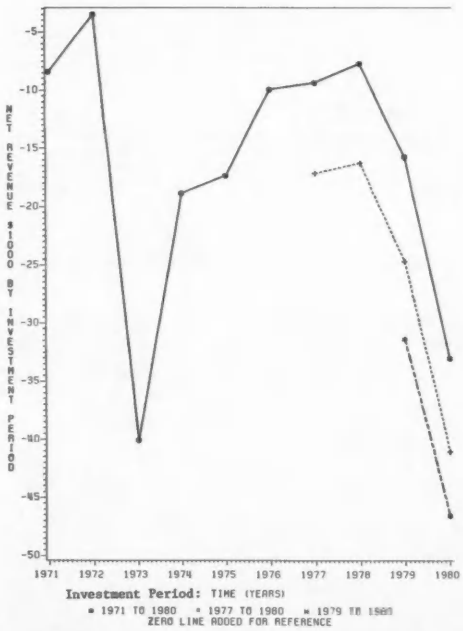
NET REVENUE $1000 BY INVESTMENT PERIOD
Investment Period: TIME (YEARS)
* 1971 TO 1980 + 1977 TO 1980 × 1979 TO 1980
ZERO LINE ADDED FOR REFERENCE

FIGURE 4.—Net revenue for a wooden vessel 18.6 to 20.0 m long operating out of Texas ports by investment period.

and high vessel costs, resulting in higher annual principal and interest payments.

SUMMARY AND CONCLUSIONS

Due to the inflationary trend in recent years, investments made in the early part of the last decade performed better than those made in the latter part. Steel vessels generally showed higher economic profits than wooden ones, and medium-sized vessels (18.6-20.0 m in overall length) were the most efficient vessels to operate in the Gulf of Mexico.

Shrimp production in the Gulf of Mexico has significant seasonal variations—periods of low shrimp landings and periods of abundant catch. Although the general trend in real prices was upward, high variability has created short-run uncertainty for shrimp producers. In general, after-tax net revenue was lowest in 1974; 1978 was the most favorable year of operation.

Vessel terminal value plays a major role in determining overall returns to investment. The NPV for the investment increased when the terminal value rose from 35 to 100% of the original vessel cost (Table 6). Based on the net present value criterion, the 18.6-20.0 m steel vessels once again proved to be the most feasible investment. Inves-

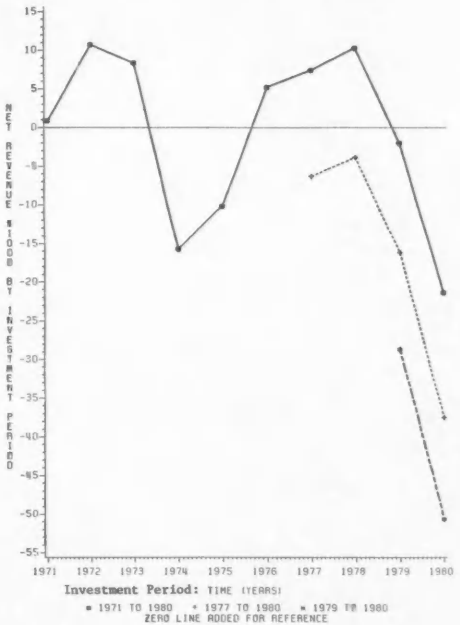

FIGURE 5.—Net revenue for a wooden vessel 20.1 to 21.5 m long operating out of Texas ports by investment period.

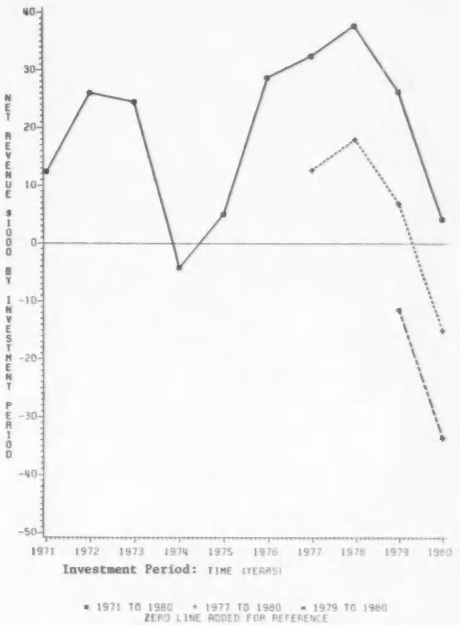

FIGURE 6.—Net revenue for a steel vessel 18.6 to 20.0 m long operating out of Texas ports by investment period.

TABLE 6.—Net present value for each investment period, salvage value, and vessel type for vessels operating out of Texas ports.

Investment period:	1971 to 1980		1977 to 1980		1979 to 1980	
Salvage value: / Vessel type	35%	100%	35%	100%	35%	100%
Wooden, 17.1-18.5 m	−14,303	4,113	−16,166	2,019	−17,766	4,122
Wooden, 18.6-20.0 m	−70,622	−37,348	−49,898	−30,731	−32,431	−17,612
Wooden, 20.1-21.5 m	4,993	23,089	−18,368	6,834	−27,829	−9,667
Steel, 18.6-20.0 m	89,154	106,585	51,483	84,543	16,250	44,462
Steel, 20.1-21.5 m	22,572	42,560	12,759	47,954	−9,355	18,140
Steel, 21.6-23.0 m	13,385	35,352	−18,161	19,655	−27,528	1,212

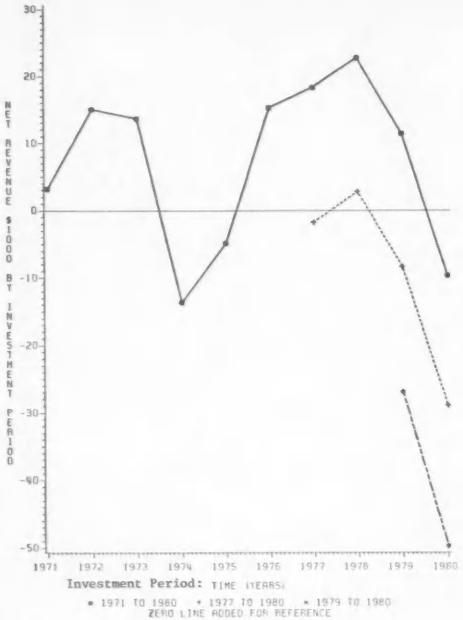

FIGURE 7.—Net revenue for a steel vessel 20.1 to 21.5 m long operating out of Texas ports by investment period.

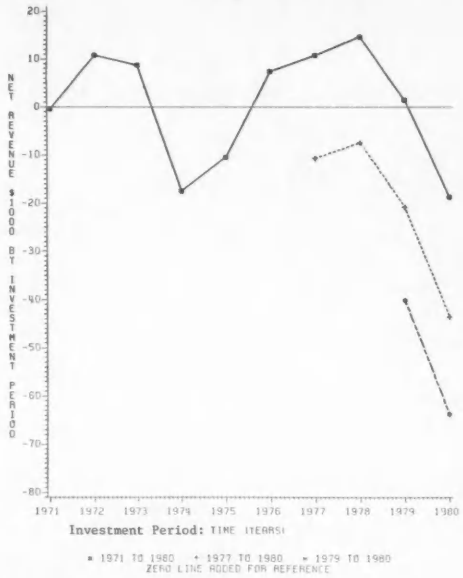

FIGURE 8.—Net revenue for a steel vessel 21.6 to 23.0 m long operating out of Texas ports by investment period.

tors should, however, bear in mind that based on this sample data similar-sized vessels built of wood are not feasible ventures.

It can be inferred from this study that in high inflationary periods, shrimp producers should avoid newly financed vessels. The resultant increases in costs of equity and debt capital are such that economic profit is eliminated. Investing in used vessels may be a viable alternative.

Results from this study further indicate that the economic performance of steel vessels is far superior to that of wooden vessels. Steel vessels can withstand adverse weather conditions much better than wooden ones and as a result, can spend longer days in offshore fishing. Steel vessels showed higher landings per trip than similar-sized wooden vessels. Therefore, the extra expense to purchase steel vessels may prove a worthy investment.

ACKNOWLEDGMENTS

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QUANTITATIVE AND QUALITATIVE BACTERIOLOGY OF ELASMOBRANCH FISH FROM THE GULF OF MEXICO[1]

JOHN D. BUCK[2]

ABSTRACT

Twelve species of elasmobranch fish (8 sharks, 2 rays, 1 skate, and 1 guitarfish) taken from the Gulf of Mexico off Sarasota, Florida, were studied. Numbers of bacteria on skin were recorded, as were types of bacteria occurring on skin, gills, teeth, and in intestinal contents. Comparative observations were made on eight species of osteichthyan fish and seawater. Counts/cm² of elasmobranch skin varied greatly both among genera and within a given species. In general, skin displayed relatively high counts which could be of significance in subsequent flesh spoilage. One brief study of spoilage of nurse shark meat at 5°C and room temperature (24°-26°C) showed that, after 7 days, species of *Pseudomonas*, *Vibrio*, and *Micrococcus* were dominant at the lower temperature while *Micrococcus* and *Proteus vulgaris* were recovered at 24°-26°C. Various types of bacteria found in or on the several areas of elasmobranch fish examined were compared with the little information available in the literature. Overall, Gram negative bacteria, particularly the genera *Pseudomonas* and *Vibrio*, were most common although several species of Gram positive bacteria were found also. *Planococcus* isolates from skin may represent important organisms because they have been implicated in shrimp spoilage. Three genera of hemolytic bacteria (*Proteus*, *Staphylococcus*, *Streptococcus*) were recovered from teeth of several elasmobranchs and may present a hazard to bite victims. Also, a variety of enteric bacteria potentially pathogenic to humans was found in intestinal contents; therefore, caution is suggested in handling shark material.

Considerable information is available on the normal and spoilage microflora of marine fish (e.g., Shewan 1961, 1971; Horsley 1977). However, the bacteriology of the elasmobranchs (sharks, skates, rays) is less understood despite a widespread present commercial fishery in local areas (Riedel 1961; McCormick et al. 1963) and its future potential (Juhl 1973; U.S. Department of Commerce 1982). Venkataramen and Sreenivasan (1955) studied the bacterial flora of skin of one shark caught off India; Johnson et al. (1968) characterized the intestinal microflora of five species of sharks obtained in the Indian Ocean; and Yap (1979) reported on skin isolates of two sharks freshly caught off Australia. Liston (1957) studied the bacteria associated with slime and gills of fresh North Sea skate. Spoilage bacteria in shark flesh were noted by Wood (1950) in Australia and Velankar and Kamasastri (1955) in India. Although the number of shark attacks on humans worldwide is statistically small (Baldridge 1974; Coppleson 1975), there are no substantive data on the potential bacteriological hazard of shark bites other than brief notations of hemolytic bacteria being recovered from the teeth of sharks (Davies 1960; Davies and Campbell 1962).

Consequently, this study was initiated to characterize the numbers and types of bacteria associated with a wide variety of elasmobranch fish common to the Gulf of Mexico. Comparative data were recorded for water and osteichthyan fish caught in the same area. These results will have relevance to the potential spoilage of elasmobranch meat and the pathobiology of shark bites.

METHODS

Sampling Sites

All fish were obtained from the Gulf of Mexico within several kilometers off Sarasota, Fla., or in the contiguous waters of Sarasota Bay. Small elasmobranchs were caught by use of a long, monofilament gill net set from the surface to a depth of about 1 m. Larger sharks were caught using baited longlines farther offshore. The one sand tiger shark, *Odontaspis taurus*, studied was obtained from the Mystic Marinelife Aquarium (Mystic, Conn.) and had been dead and refrigerated for 4 h. This shark, caught off the coast of New Jersey 3 d previously, was maintained in chlorinated brine water at the aquarium for 2 d

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prior to death. Only teeth and intestinal contents were sampled. For comparative bacteriological studies, several osteichthyan fish were caught by rod and reel or retrieved from the gill net mentioned above. Some elasmobranchs were occasionally maintained in large concrete or fiberglass tanks containing seawater piped from Sarasota Bay. All fish examined from tanks were either alive or had been dead for less than 1 h. Fish caught in the Gulf of Mexico were either iced if dead or kept in a wet hold until examined, which was routinely less than 1 h. In one case (see below) sharks were dead for 3 h before sampling. Water samples were collected from either Sarasota Bay or the tanks containing fish.

Quantitative Analysis

Swabbing was compared initially with two other methods involving the use of membrane filters in a quantitative sampling of elasmobranch skin. In the swabbing technique, a sterile aluminum foil template containing a 3.1 × 3.1 cm square opening (9.6 cm^2) was placed on the skin, on the side of each fish just posterior to the gills. A sterile polyester-tip swab (Falcon No. 2069[3]) was used over the exposed area in all directions, and the tip was broken off in a screw-capped tube containing 10 ml of sterile seawater. Decimal dilutions of this were prepared in 9 ml of sterile seawater and 0.1 ml volumes spread (Buck and Cleverdon 1960) on Bacto-Marine Agar (Difco Laboratories, Detroit, Mich.). One procedure with membrane filters involved placing sterile 0.45 μm gridded membranes (Millipore No. HAWGO47SO) on shark skin and pressing them down by rolling a sterile glass rod across the membrane. The membrane was then placed grid uppermost on the surface of an agar plate. The second membrane filter technique was similar to the first except that the membrane, after exposure to the skin, was placed in a sterile plastic screw-cap centrifuge tube with sterile seawater and agitated on a vortex mixer for 30 s. Decimal dilutions and platings were then made as indicated above. All plates were incubated at room temperature (24°-26°C) for 3-5 d. Counts/cm^2 of skin were calculated.

Qualitative Analysis

In addition to skin, other body areas including teeth, gills, and intestinal contents were sampled by use of a swab. The upper third of plates of eosin-methylene blue, tryptic-soy, brain heart infusion, and marine agar (all Difco) was swabbed, and the remaining two portions of the plate were streaked sequentially with a sterile wire loop to isolate colonies. Plates were incubated at room temperature (24°-26°C) and 37°C for 1-5 d and colonies were selected based on differences in morphology.

Qualitative changes in the bacterial flora on shark flesh were assessed as a function of time and temperature. Pieces of nurse shark, *Ginglymostoma cirratum*, flesh (about 2 cm^2) were cut aseptically from one area of one side of the fish after the skin had been removed. These pieces were placed in sterile petri dishes and incubated at room temperature (24°-26°C) and 5°C. Initially and after 3, 4, 5, and 7 d incubation, the surface of the flesh was sampled using a sterile loop, which was used to directly inoculate agar plates to obtain well-isolated colonies.

Tank and bay samples were collected at a depth of about 30 cm in sterile bottles. One ml volumes were diluted in 9 ml of sterile seawater and additional decimal dilutions prepared in a similar manner. Spread plates (see above) were made on marine agar. Representatives of various colonial types were selected and identified after incubation for 3-5 d at room temperature.

All isolates were maintained on slants of either marine agar or tryptic-soy agar. Gram reactions were recorded by both conventional staining and the KOH technique (Buck 1982). Gram negative enteric bacteria were identified using either the Enterotube II (Roche Diagnostics, Nutley, N.J.) or API 20E (Analytab Products, Plainview, N.Y.) systems. Hemolysis was detected on tryptic-soy agar containing 5% horse blood. Other bacteria were characterized using the methods of Shewan et al. (1960) and Oliver (1982).

RESULTS AND DISCUSSION

Quantitative Analysis

Counts by the swab technique averaged 115% higher than those obtained by membrane filters applied directly to agar plates (two experiments) and 910% higher than counts by agitating the membrane in seawater followed by dilution and plating (three experiments). All subsequent counts of skin bacteria on both elasmobranch and osteichthyan fish were made using the swab

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

technique (Yap 1979), although this technique has inherent weaknesses (Horsley 1977), especially in examining shark skin, because it is abrasive and essentially three-dimensional. Nonetheless, counts obtained by swabbing a known area were always higher than those achieved by pressing a membrane filter on the skin, probably because the membrane did not recover bacteria associated with the lower portion of the denticles. The fibrous texture of the swab, while prone to some shredding unless care was used, may have allowed penetration into the skin. Perhaps an agar-coated slide or "paddle" which could be pressed onto shark skin would be more effective, although such a procedure might be unwieldy in the field.

Table 1 shows the number of bacteria recovered from the skin of various elasmobranch and osteichthyan fish. Elasmobranch skin showed a very wide range of counts both among genera and within a given species. Data in Table 1 indicated that there was no obvious correlation between bacterial counts on tank-held and freshly caught elasmobranchs, although bacterial counts on skin of three tank-held Atlantic sharpnose sharks were about two orders of magnitude lower than counts for one specimen of the same species caught in a gill net. Three of the highest counts on shark skin noted in Table 1 (bonnethead, 410,000/cm²; blacktip, 530,000/cm²; blacknose, 330,000/cm²) were from fish which had been dead for 3 h. This suggests that bacteria rapidly colonize skin of dead sharks. Yap (1979) reported varying counts on skin of freshly caught shark which depended on the area of the fish sampled. His counts (310-1,900/cm²) were, in general, lower than those reported herein, and were estimated from broth dilutions and not plates. The shark skin sampled here displayed relatively high bacterial counts which are of considerable significance if the sharks are to be used for food. Large numbers of bacteria could be deposited onto flesh which subsequently may undergo more rapid spoilage if not adequately washed and/or refrigerated. With the exception of the bighead searobin, *Prionotus tribulus*, the counts on osteichthyan fish were quite similar and within the range reported in other studies (Horsley 1977).

TABLE 1.—Number of bacteria on fish skin (Bacto-marine agar).

Taxon	Source	No./cm²
Elasmobranchs		
Florida smoothhound, *Mustelus norrisi*	Gill netted	[1]120 [1]840
Nurse shark, *Ginglymostoma cirratum*	Gill netted	[1]8,200
Atlantic sharpnose shark, *Rhizoprionodon terraenovae*	Gill netted	[1]2,300 220,000 [1]1,000 [1]1,000
Bonnethead or shovelhead shark, *Sphyrna tiburo*	Gill netted	400,000 42,000 1,100 410,000
Brown or sandbar shark, *Carcharhinus plumbeus*	Longline caught	2,300
Blacktip shark, *Carcharhinus limbatus*	Gill netted	530,000
Blacknose shark, *Carcharhinus acronotus*	Gill netted	330,000
Tiger shark, *Galeocerdo cuvieri*	Longline caught	240
Atlantic guitarfish, *Rhinobatos lentiginosus*	Gill netted	[1]260 [1]460
Clearnose skate, *Raja eglanteria*	Gill netted	[1]100,000 80,000
Southern stingray, *Dasyatis americana*	Gill netted	[1]6,700
Cownose ray, *Rhinoptera bonasus*	Gill netted	50,000
Osteichthyes		
Gulf menhaden, *Brevoortia patronus*	Gill netted	23,000
Southern flounder, *Paralichthys lethostigma*	Rod caught	26,000
Spanish mackerel, *Scomberomorus maculatus*	Gill netted	15,000
Ladyfish, *Elops saurus*	Gill netted	19,000
Searobin, *Prionotus tribulus*	Gill netted	100
Black drum, *Pogonias cromis*	Gill netted	15,000
Permit, *Trachinotus falcatus*	Gill netted	7,100
Atlantic spadefish, *Chaetodipterus faber*	Gill netted	14,000

[1]Tank held.

Qualitative Analysis

Table 2 shows the number of isolates and genera of bacteria recovered from elasmobranch and osteichthyan fish and from waters where the fish were taken or held. The Gram negative bacteria, especially *Pseudomonas*, *Vibrio*, and *Cytophaga*, accounted for 89% of the 111 isolates from skin. In other studies, pigmented Gram positive isolates of *Micrococcus*, *Bacillus*, and *Corynebacterium* were the most common (30 strains) on the skin of one shark (*Carcharhinus* sp.) caught off India; only 5 cultures of Gram negative *Achromobacter*, *Flavobacterium*, and *Vibrio* were recovered (Venkataraman and Sreenivasan 1955). *Pseudomonas* (40%), Micrococcaceae (30%), and *Moraxella* (15%) were dominant on skin of a freshly caught shark off Australia (Yap 1979). The data here for skin (Table 2) show a similar percentage for *Pseudomonas* but considerably fewer isolates of *Moraxella* and Gram positive cocci.

Table 2 shows that for Gulf of Mexico sharks, fewer genera were recovered from intestines than from other areas, but that the Gram negative genera were predominant and species of *Photobacterium*, *Pseudomonas*, and *Vibrio* accounted for 57% of the isolates. Gram positive bacteria (one

TABLE 2.—Number of isolates and percentage of bacterial genera recovered from elasmobranch and osteichthyan fish and water of the Gulf of Mexico.

	Elasmobranchs								All elasmobranch samples		Osteichthyes skin		Water	
	Skin		Gills		Teeth		Intestines							
Genus	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Gram negative														
Aeromonas	1	1			2	3			3	1			2	4
Acinetobacter	4	4	2	10	6	8	1	7	13	6	3	7		
Alcaligenes	2	2	1	5					3	1	2	5	4	8
Cytophaga	11	10	1	5	1	1	1	7	14	6	1	2		
Flavobacterium	1	1			4	5	1	7	6	3	1	2		
Flexibacter	1	1							1	1				
Moraxella	4	4			1	1			5	2	2	5	3	6
Photobacterium	4	4	4	18	5	7	4	29	17	8			6	12
Pseudomonas	35	32	1	5	10	13	2	14	48	22	8	18	15	30
Vibrio	30	27	10	46	17	23	2	14	59	27	16	36	15	30
Xanthomonas	6	5	1	5	2	3			9	4	4	9	2	4
Gram positive														
Arthrobacter	4	4			3	4	1	7	8	4			1	2
Bacillus					4	5	1	7	5	2	4	9	1	2
coryneforms	1	1	1	5	1	1			3	1	2	5	1	2
Micrococcus-Staphylococcus	4	4	1	5	8	11			13	6	2	5	1	2
Planococcus	3	3			2	3			5	2				
Streptococcus					9	12	1	7	10	5				
Total	111		22		75		14		222		45		51	

isolate each of *Arthrobacter, Bacillus*, and *Streptococcus*) represented 21% of the total. In a study of intestinal material from five species of sharks caught in the Indian Ocean, 10 isolates of *Bacillus* were found, and 1 each of *Corynebacterium, Alcaligenes, Vibrio, Spirillum*, and *Xanthomonas*; one animal showed no bacteria (Johnson et al. 1968).

No data are available in the literature on bacterial types recovered from shark gills, although the gills and skin of North Sea skates have been studied (Liston 1957). Gram negative bacteria were dominant with *Pseudomonas* most common on both skin and gills. Qualitative observations of skin agreed with the present data (Table 2), but skate gills showed a much higher percentage of *Pseudomonas* (60%) compared with this study (5%). The other Gram negative bacteria from skate gills were also found in this study (Table 2).

Hemolytic bacteria were isolated from the teeth of sharks in the present study. *Streptococcus* spp. were recovered from teeth of shovelhead, *Sphyrna tiburo*, and sand tiger, *Odontaspis taurus*, sharks; *Staphylococcus* spp. were found on the teeth of a cownose ray, *Rhinoptera bonasus*; and *Providencia rettgeri* was recovered from teeth of two shovelhead sharks. All of these bacteria were from sharks taken in the Gulf of Mexico except for the sand tiger shark which was caught off New Jersey and had been in captivity for only 3 d. In addition, several hemolytic species of *Vibrio* have been isolated recently from the teeth of a white shark, *Carcharodon carcharias*, caught off Block Island, R.I. (Buck et al. unpubl. data[4]).

Hemolytic bacteria were found in the mouths of sharks from South African waters, and it was suggested that bacterial infections of bites could have been a contributing factor in the deaths of victims (Davies 1960). The hemolytic bacterium recovered from teeth of *Carcharhinus zambezensis* (*leucas*?) was described as a "Paracolon bacillus" (Davies and Campbell 1962).

The present observations not only confirm the occurrence of hemolytic organisms on teeth of sharks in nature but also extend these types to include bacteria not reported previously from sharks and the number of species of sharks which harbor them. They suggest that shark bites could possibly introduce potentially pathogenic bacteria into the tissues of victims.

A variety of enteric bacteria was found associated with the intestinal contents and occasionally the teeth of elasmobranchs; none were recovered from the gills or skin. These data are presented in Table 3. Three cultures only, all *Shigella* species, were isolated from bony fish. One was found in pinfish, *Lagodon rhomboides*, intestine, and two strains were isolated from a black drum, *Pogonias cromis*—one on the gills and the other from intestinal contents.

[4]Buck, J. D., S. Spotte, and J. J. Gadbaw, Jr. Manuscr. in prep. Bacteriology of the teeth from "Jaws": Medical implications for shark-bite victims.

Enterobacteria are found frequently on osteichthyan fish, but there are no reports in the literature on their occurrence in (on) elasmobranchs. If waters contain domestic wastes, then the fish will almost certainly be contaminated also (Shewan 1971; Horsley 1977). Coliform counts in Sarasota Bay are generally low, although counts of 1,800/100 ml have been recorded in one bayou receiving treated sewage effluent (Buck, unpubl. data[5]). Areas north (Tamplin et al. 1982) and south (Peterson and Yokel 1983) of Sarasota Bay have shown the presence of potentially pathogenic enteric bacteria. Consequently, the elasmobranch fish studied here may well have been in contact with sources of enterobacteria. The enteric bacteria encountered on the teeth and in the intestines of several elasmobranchs probably reflected feeding habits and originated on smaller prey which had passed through waters receiving human and/or animal excretions. Enteric bacteria do not multiply in passage through rainbow trout but temperature may be an important factor (Lesel and Peringer 1981; Lesel and LeGac 1983). The internal temperature of some sharks (Lamnidae) (Carey et al. 1981; Smigh and Rhodes 1983) is significantly warmer than the surrounding water. In subtropical areas, increased water temperature and that of the interior tissues of elasmobranchs might provide an environment that encourages bacterial multiplication, including potential pathogens. While none of the enterobacteria, except perhaps *Shigella* species, recovered from intestines and teeth of elasmobranchs represent primary pathogens, members of the other genera are commonly found as secondary or opportunistic pathogens in humans. Thus, caution should be exercised when handling dead shark material, particularly internal organs such as the digestive tract.

The genera *Vibrio* and *Pseudomonas* were predominant bacteria in combined data for all elasmobranch samples (Table 2). When isolates for tank-held and open-water fish were compared, these two genera were the most common in each group. The occurrence of other microbes did not vary more than 6% for any genus of bacteria between tank-held and freshly caught elasmobranchs, except for *Photobacterium* species which represented 11% of the isolates from the former and 3% of the latter.

The bacterial flora of osteichthyan fish and seawater consisted largely of Gram negative bacteria (82% and 94%, respectively), with *Vibrio* and *Pseudomonas* predominating. No substantial differences in generic composition were noted between Sarasota Bay water and fish holding tanks. Fewer numbers of several other Gram negative forms were found; these results agree with those of others (e.g., Shewan 1961). Small populations of Gram positive bacteria (*Arthrobacter, Bacillus*, cocci) were noted and probably represented terrestrial influence because the fish were taken from nearshore waters. This assumption may require reevaluation because there may be a widespread distribution of Gram positive bacteria in seawater (Gunn et al. 1982).

The microflora of spoiling shark muscle (no species indicated) from Australia have been studied, and the genus *Corynebacterium* was the dominant organism; *Pseudomonas* species and Gram positive cocci were also found in large numbers (Wood 1950). Few coryneforms were isolated in the present study, although *Pseudomonas* and Gram positive organisms were commonly recovered. In the brief study here of nurse shark flesh, the dominant bacteria found initially were species of *Vibrio* and *Pseudomonas*. After 7 d of incubation at 5°C, the flora were composed principally of *Pseudomonas, Vibrio*, and *Micrococcus*. When flesh was held at room temperature (24°-26°C), Gram positive cocci and *Proteus vulgaris* were

[5]J. D. Buck, University of Connecticut Marine Research Laboratory, Noank, Conn., unpubl. data, 1982.

TABLE 3.—Enterobacteriaceae isolated from elasmobranch fish.

Taxon	Bacteria
Nurse shark, *Ginglymostoma cirratum*[1]	*Proteus vulgaris*
Intestine	*Escherichia coli*
Shovelhead shark, *Sphyrna tiburo*	
Intestine	*Enterobacter agglomerans*
	Escherichia coli
	Shigella sp.
Teeth	*Citrobacter freundii*
	Providencia rettgeri
	Providencia sp.
Sandbar shark, *Carcharhinus plumbeus*	
Intestine	*Shigella* sp.
Teeth	*Proteus vulgaris*
	Providencia rettgeri
Blacktip shark, *Carcharhinus limbatus*	
Intestine	*Escherichia coli*
	Providencia alcalifaciens
	Shigella sp.
Teeth	*Escherichia coli*
	Proteus vulgaris
Sand tiger shark, *Odontaspis taurus*[1]	
Intestine	*Citrobacter freundii*
	Morganella morganii
	Proteus vulgaris
Cownose ray, *Rhinoptera bonasus*	
Intestine	*Shigella* sp.
Teeth	*Serratia liquefaciens*
Clearnose skate, *Raja eglantera*[1]	
Intestine	*Escherichia coli*

[1]Tank held.

predominant after 7 d. The latter is capable of hydrolyzing urea, and several species of *Micrococcus* are urease-positive (Buchanan and Gibbons 1974); hence, both of these groups are potential contributors to shark tissue spoilage. This enrichment of Gram positive types in elasmobranch spoilage was noted by Wood (1950).

Bacteria were found in 12 samples of shark muscle (*Scoliodon* sp.) allowed to spoil at 27°-30°C (Velankar and Kamasastri 1955). No coryneforms and only one *Micrococcus* isolate were found; all others were unidentified Gram negative nonpigmented rods.

The spoilage of iced abdominal wall muscle of Australian school shark, *Galeorhinus australis*, was studied by Yap (1979). *Pseudomonas* and *Moraxella* (45% and 20%, respectively) were the dominant bacteria recovered after 10 d although the Gram positive cocci represented 15% of the total.

The data presented here for the flesh spoilage experiment, albeit limited, confirm the observations of Wood (1950) and Yap (1979), but none of these parallel the findings of Velenkar and Kamasastri (1955) which also concerned sharks from subtropical waters. Perhaps the local marine microflora or experimental conditions influenced their observations.

Although the number of isolations was relatively small, the genus *Planococcus* was found associated with elasmobranch skin and teeth in this study. All the cultures recovered were yellow-pigmented and were probably *Planococcus citreus*, the only accepted species (Buchanan and Gibbons 1974). This proteolytic bacterium has been implicated in shrimp spoilage (Alvarez 1982) and may be a significant spoilage organism of elasmobranch flesh.

CONCLUSIONS

The observations reported here have shown that elasmobranch fish contain a large and diverse bacterial flora. Because there is little information on the microbiology of sharks, skates, and rays, assessing the relative significance of the data is difficult. In many cases, counts of bacteria on the skin were an order of magnitude higher than those noted on osteichthyan fish caught in the same waters. In other samples, counts were two orders of magnitude lower. Considerable variation was seen in individual species of elasmobranchs. Types of bacteria recovered from different areas of fresh fish and during one controlled spoilage experiment on flesh did not correlate well in all respects with results of other studies which in some instances were limited to one or a few fish or different species than those considered here. Also, little information was provided in the literature on cultural conditions and other variables which could affect development of various bacteria reported. The data here substantiate the occurrence of certain potential spoilage bacteria on skin and include the genus *Planococcus* which has been implicated in shrimp spoilage. The present study also confirms and extends other observations on the occurrence of hemolytic bacteria on shark teeth. In addition, potentially pathogenic enterobacteria were recovered from teeth and intestinal contents of several elasmobranch species. It is hoped that future studies will include larger numbers of additional shark species for a clearer assessment of the role of bacteria in both spoilage and public health aspects of a valuable and underutilized marine resource.

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DISTRIBUTION AND FEEDING OF THE HORSESHOE CRAB, *LIMULUS POLYPHEMUS*, ON THE CONTINENTAL SHELF OFF NEW JERSEY[1]

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ABSTRACT

The horseshoe crab, *Limulus polyphemus*, population was assessed during hydraulic dredge surveys of the surf clam resource in the inshore 5.5 km (3 nautical miles) of the continental shelf off New Jersey from 1976 through 1979. Frequency of occurrence and abundance was higher off the southern half of the state, which may be a function of its proximity to Delaware Bay, a principal spawning site. Horseshoe crabs consumed various benthic organisms, primarily bivalves, arthropods, and polychaetes. Surf clams, *Spisula solidissima*, were important in the diet of *Limulus*; individual valves ranged in length from <1 mm to about 35 mm. In the laboratory, horseshoe crab predation was observed on surf clams as long as 46 mm.

This report describes the distribution of the horseshoe crab, *Limulus polyphemus*, on the inshore continental shelf off New Jersey, and the diets of a sample of these animals. Previous studies of the horseshoe crab on the continental shelf are limited to distributional records (Wolff 1977; Shuster 1979) or tagging studies conducted close to estuarine spawning areas (Baptist et al. 1957; Rudloe 1980), although crabs have been found at depths as great as 200 m according to National Marine Fisheries Service surveys (J. W. Ropes[4]).

Since the early 1960's, an intensive surf clam, *Spisula solidissima*, fishery has developed along the New Jersey coast (Ropes 1982). The junior author (Haskin) and his colleagues have inventoried the surf clam resource in the New Jersey waters, to 5.5 km (3 nmi) offshore yearly since 1972. All macroinvertebrates, including *L. polyphemus*, captured in hydraulic dredge hauls from 1976 through 1979 were counted. Since a percentage of the horseshoe crab population migrates from the continental shelf to estuaries and back again (Shuster 1982), we analyzed both temporal and spatial variability. Separating these effects was difficult because the sampling program was designed primarily to inventory a sessile clam resource, rather than a migratory one. However, the data, based on over 1,100 stations, still represent the most systematic survey of *L. polyphemus* distribution on the inshore continental shelf, and since exploitation of these crabs for biomedical research and bait is increasing (Pearson and Weary 1980), our study provides baseline information should future population assessment studies be warranted.

Information on the feeding biology of horseshoe crabs is limited (Lockwood 1870; Fowler 1908; Shuster 1950; Smith and Chin 1951; Smith 1953; Smith et al. 1955; Botton 1981). In this study, stomach contents from 36 horseshoe crabs from the continental shelf were examined to supplement a more intensive study of the food habits of animals from Delaware Bay (Botton 1982); in August 1980, predation by crabs on surf clams about 4 cm long was examined in the laboratory.

MATERIALS AND METHODS

Population Survey

Stations were sampled with a hydraulic dredge (Meyer et al. 1981), adjusted to retain surf clams >88 mm. This gear retained both adult and subadult horseshoe crabs. Catch data, as number of animals per tow, were normalized for dredge width and tow time. The standard tow (ST) is defined as a 5-min haul using a 152 cm knife (width of dredge).

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[4]J. W. Ropes, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543, pers. commun. February 1983.

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This standard tow covered an area of about 418 m².

The New Jersey coastline from Cape May to Shark River Inlet was subdivided into 19 areas (Table 1). Stations were located by 3-point sextant fixes and/or loran C, and grouped in intervals of 0-1.8 km (0-1 nmi) (0-0.9 and 0.9-1.8 km north of Beach Haven Inlet), 1.8-3.7 km (1-2 nmi) and 3.7-5.5 km (2-3 nmi) based on distance from land. Inlets were used as latitudinal break points (Fig. 1). Because of the reduced sampling effort from 1.8 km offshore, these areas were larger than areas inshore of 1.8 km.

For statistical analysis, all tows on the same day in a given area were considered replicates. The Analysis of Variance (ANOVA) for the number of crabs per tow had three sources of variation: Area, time nested within area, and replicate tow nested within time within area. Because each year's design was unbalanced, a pseudo-F procedure (Hicks 1973) tested the significance of the area effect. Data were log-transformed to stabilize the variances. When areas were sampled more than once in a given year, we tested differences between sample dates using a completely randomized one-way classification ANOVA. If the F-test was significant, a Student-Neumann-Keuls procedure for unequal group sizes tested for differences between the means for each sample date (Zar 1974).

TABLE 1.—Description of areas of the New Jersey coast surveyed from 1976 to 1979.

Distance offshore (km)	Area	Southern boundary	Northern boundary
0-1.8	1	Cape May Inlet	Hereford Inlet
	2	Hereford Inlet	Stone Harbor
	3	Stone Harbor	Townsends Inlet
	4	Townsends Inlet	Corson Inlet
	5	Corson Inlet	Great Egg Harbor Inlet
	6	Great Egg Harbor Inlet	Absecon Inlet
	7	Absecon Inlet	Beach Haven Inlet
	8	Beach Haven Inlet[1]	Barnegat Inlet
	9	Beach Haven Inlet[2]	Barnegat Inlet
	10	Barnegat Inlet	Shark River Inlet
	11	Barnegat Inlet[2]	Shark River Inlet
1.8-3.7	12	Cape May Inlet	Townsends Inlet
	13	Townsends Inlet	Absecon Inlet
	14	Absecon Inlet	Beach Haven Inlet
	15	Beach Haven Inlet	Shark River Inlet
3.7-5.5	16	Cape May Inlet	Townsends Inlet
	17	Townsends Inlet	Absecon Inlet
	18	Absecon Inlet	Beach Haven Inlet
	19	Beach Haven Inlet	Shark River Inlet

[1]0-0.9 km.
[2]0.9-1.8 km.

Stomach Contents

Thirty-six adult *L. polyphemus* were collected between 10 July and 25 August 1978 for analysis of stomach contents. The results are grouped for three locations: Stone Harbor (1 station, 5 individuals), Atlantic City (12 stations, 24 individuals), and Point Pleasant (3 stations, 7 individuals) (Fig. 1).

Complete digestive tracts were removed from crabs aboard ship or shortly after returning to the laboratory, fixed in 10% Formalin[5] seawater, and later transferred into 70% ethanol until examination. Food, much of which was entangled with mucus, was sorted under a 10× stereoscope. The number of bivalves was determined by counting the number of umbones and dividing by 2. Shells were measured by ocular micrometer or vernier caliper.

RESULTS

Population Surveys

1976 Survey

Sampling commenced in mid-July and was most extensive in late August and early September; no areas north of Beach Haven Inlet were sampled. Horseshoe crabs were present in over 90% of all hauls in the first 1.8 km between Hereford Inlet and Townsends Inlet, and from 1.8 to 3.7 km between Cape May and Townsends Inlet (Table 2). More than 10 animals/ST were dredged from 1.8 to 3.7 km offshore between Cape May and Absecon

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—1976 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	*N* stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	27	85.2	7.7	0.81	25.7
	2	12	66.7	4.1	1.27	10.7
	3	21	90.5	6.0	0.65	15.0
	4	7	71.4	11.2	1.14	35.3
	5	9	88.9	4.8	1.05	15.0
	6	8	62.5	2.4	1.01	5.4
	7	10	70.0	7.2	1.01	20.0
1.8-3.7 km	12	31	90.3	14.6	0.69	47.1
	13	28	78.6	12.5	2.36	145.7
	14	10	80.0	3.0	0.68	6.0
3.7-5.5 km	16	18	83.3	6.6	0.97	26.8
	17	16	62.5	25.4	2.72	277.4
	18	7	42.9	1.1	1.30	3.2

Analysis of Variance:

Source	df	SS	MS	*F*	*P*
Total	202	259.94			
Area	12	40.08	3.34	1.12	ns
Time (area)	38	80.77	2.13	2.32	0.05
Station (time (area))	152	139.09	0.92		

FIGURE 1.—Map of the New Jersey coast. Filled circles show the locations of stations from which *Limulus polyphemus* stomach contents were obtained.

Inlets, and in several areas from 0 to 1.8 km and 3.7 to 5.5 km between these two inlets. Two hundred seventy-seven crabs were found in a single dredge tow, 5.4 km off Townsends Inlet.

In 1976, both time within area and station within time within area were greater sources of variability than area itself (Table 2). The inshore 1.8 km from Cape May to Hereford Inlets was sampled on 10 and 30 July and again on 4-5 September. The mean number of crabs collected per standard tow on each date was 8.3, 9.3, and 2.1, respectively ($F = 2.86$, $0.10 < P < 0.05$). There were no significant differences between sampling dates within any other individual areas.

1977 Survey

Most sampling in southern New Jersey was done in June and July, but the areas north of Beach Haven Inlet were sampled in August. Thus, temporal variability was confounded with geographic variability. Areas north of Beach Haven Inlet were

relatively depauperate; the area effect was significant at $P < 0.07$ (ANOVA); the time within area effect was significant at $P < 0.05$ (Table 3).

Limulus polyphemus occurred in 70% to 100% of all tows between Cape May and Absecon Inlet (Table 3). Crabs were most numerous from 0 to 1.8 km offshore between Cape May and Hereford Inlets. When sampled on 15 June (23 stations), there was an average of 15.52 crabs/ST, but in late August-early September (9 stations), only 2.17 crabs/ST ($F = 5.006, P < 0.05$). Abundance from 1.8 to 3.7 km between Cape May and Townsends Inlets declined over the same time, from 13.08 to 3.3 crabs/ST ($F = 4.805, P < 0.05$). From 1.8 to 3.7 km offshore, between Townsends Inlet and Absecon Inlet, crabs declined between early July ($\bar{x} = 25.33$, $n = 6$), late July-early August ($\bar{x} = 3.95$, $n = 14$), and late August ($\bar{x} = 7.6$, $n = 5$), but the differences were marginally significant ($F = 3.03$, $0.10 < P < 0.05$).

Horseshoe crabs were encountered in every tow in the first 1.8 km from Beach Haven Inlet to Barnegat Inlet, although the average abundance was only 5 crabs/ST. No other area north of Atlantic City contained over 4 crabs/ST and an onshore-offshore gradient was particularly evident between Beach Haven Inlet and Shark River Inlet. From 1.8 to 3.7 km offshore, crabs were found in only 40% of the tows, and from 3.7 to 5.5 km, no crabs were present at seven stations.

TABLE 3.—1977 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	*N* stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	34	94.1	11.3	1.41	87.0
	2	10	70.0	2.8	1.29	12.0
	3	16	93.8	7.0	0.83	20.6
	4	17	100.0	6.1	0.68	14.2
	5	8	100.0	5.9	0.64	12.0
	6	8	75.0	2.9	0.89	7.0
	7	8	75.0	2.0	0.82	4.0
	8	12	100.0	6.0	0.79	19.6
	9	4	100.0	4.4	0.28	6.0
	10	25	60.0	2.2	1.62	13.9
	11	4	75.0	2.6	1.22	7.1
1.8-3.7 km	12	25	84.0	5.5	1.61	44.0
	13	25	92.0	9.8	1.96	97.0
	14	7	100.0	4.1	0.79	10.0
	15A[1]	9	44.0	1.6	1.34	5.4
	15B[2]	6	33.3	0.9	1.93	4.3
3.7-5.5 km	16	26	96.1	9.6	0.76	22.4
	17	9	77.8	7.6	1.44	33.0
	18	9	44.4	3.0	1.82	16.6
	19	7	0.0	0.0	—	0.0
Analysis of Variance:						
Source		df	SS	MS	*F*	*P*
Total		261	258.36			
Area		19	76.05	4.00	1.79	0.07
Time (area)		32	50.07	1.56	2.48	0.05
Station (time (area))		210	132.23	0.63		

[1]Beach Haven Inlet to Barnegat Inlet.
[2]Barnegat Inlet to Shark River Inlet.

1978 Survey

As in 1977, the areas north of Beach Haven Inlet were sampled late in the summer. Stations south of Atlantic City had many more horseshoe crabs than ones farther north, and from Beach Haven Inlet northward, few animals were encountered offshore of 1.8 km (Table 4). Area and time within area effects were significant (ANOVA, $P < 0.01$; Table 4).

Temporal variability within an area was difficult to analyze, because for most areas, either the survey was completed in a single weekend, there were low densities on all dates (north of Beach Haven), or there were small sample sizes on one or more cruises. Between Cape May and Townsends Inlet, from 3.7 to 5.5 km offshore, there were significantly more crabs on 20 July ($\bar{x} = 12.64$, $n = 11$) than on 24 June ($\bar{x} = 3.11$, $n = 9$) ($F = 26.998$, $P < 0.001$).

1979 Survey

In contrast to 1977 and 1978, sampling of the Beach Haven Inlet to Shark River Inlet region

TABLE 4.—1978 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	*N* stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	32	96.9	16.7	0.79	54.0
	2	10	90.0	12.2	0.71	24.0
	3	21	90.5	10.4	0.70	28.0
	4	14	100.0	13.4	0.46	24.0
	5	10	100.0	4.0	0.64	8.0
	6	14	50.0	2.4	2.19	20.0
	7	22	54.5	0.8	1.47	5.2
	8	13	46.2	0.9	1.28	3.0
	9	11	72.7	3.6	0.94	9.0
	10	25	64.0	2.2	1.05	6.4
	11	8	37.5	1.9	2.18	11.8
1.8-3.7 km	12	15	86.7	13.7	2.67	150.0
	13	20	85.0	3.5	1.26	20.0
	14	12	58.3	1.2	1.26	5.0
	15	12	41.7	1.0	1.90	6.4
3.7-5.5 km	16	20	90.0	8.4	0.75	20.0
	17	13	84.6	3.3	0.74	7.0
	18	9	55.6	2.3	1.56	11.0
	19	5	0.0	0.0	—	0.0
Analysis of Variance:						
Source		df	SS	MS	*F*	*P*
Total		281	347.91			
Area		18	165.30	9.18	4.38	0.01
Time (area)		35	38.72	1.11	1.76	0.01
Station (time (area))		228	143.89	0.63		

took place early in the summer, thus enabling a comparison of the southern and northern parts of the coast without a confounding effect of time. Both area (ANOVA, $P < 0.01$) and time ($P < 0.01$) effects were significant, and percent occurrence and abundance were low from Beach Haven Inlet northward, where horseshoe crabs were particularly scarce offshore of 1.8 km (Table 5). The inner 0.9 km from Barnegat Inlet to Shark River Inlet had significantly more *L. polyphemus* on 24 June ($\bar{x} = 5.48$, $n = 12$) than 17 August ($\bar{x} = 0.07$, $n = 10$) ($F = 11.913$, $P < 0.005$). From 3.7 to 5.5 km offshore between Townsends Inlet and Absecon Inlet, the density in late July ($\bar{x} = 3.24$, $n = 8$) was significantly higher than the density found on 17 May or 26 June ($\bar{x} = 0.88$, $n = 6$ and $\bar{x} = 1.4$, $n = 3$, respectively) ($F = 6.646$, $P < 0.005$). Stations on 28 August and 16 November, also contained fewer crabs ($\bar{x} = 0.19$, $n = 4$ and $\bar{x} = 0.44$, $n = 2$, respectively).

Stomach Contents

Stone Harbor individuals were collected on 24 July 1978, from a station, 13.4 m depth and 3.7 km offshore, which contained 150 *L. polyphemus*. Their digestive tracts were packed ($\bar{x} = 383.2$, range 88-791 individuals/crab) with blue mussels, *Mytilus edulis*; there were only traces of other food (three other bivalves, four brachyuran crabs, two foraminifera, and polychaete setae). The mean length of 38 whole valves was 6.3 mm, with a range from 4.2 to 9.0 mm. Virtually all remaining umbones were estimated to be from mussels in that range.

Crabs in the Atlantic City series ate a variety of food, primarily bivalves, annelids, and arthropods (Table 6). The surf clam, *Spisula solidissima*, was an important prey item, ranking first in frequency of occurrence and third in total abundance. Valves <1 mm in length were found, as were portions of a 35-40 mm shell length individual; about 62% of the valves were >4 mm. Other important bivalves were *Tellina* sp. and *Siliqua costata*. Twelve polychaete taxa were identified, of which *Nereis* sp. was the most frequently occurring, while the most abundant were unidentified Spionidae. Fifteen digestive tracts contained one or more specimens of brachyuran crabs, which in several cases were identified as young rock crabs, *Cancer irroratus*.

Stomachs of the seven horseshoe crabs from the Point Pleasant series contained little food. Only four bivalves (one *S. solidissima* and three *M. edulis*), a gastropod (*Nassarius trivittatus*), and a brachyuran were identified. Polychaete setae were

TABLE 5.—1979 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	N stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	30	96.7	20.2	1.20	107.8
	2	11	100.0	9.6	0.70	18.3
	3	21	100.0	15.5	0.63	33.3
	4	20	100.0	20.6	0.96	92.5
	5	9	100.0	9.4	0.67	19.2
	6	19	68.4	3.8	1.13	14.2
	7	20	55.0	1.4	1.15	5.1
	8	20	55.0	1.7	1.38	7.5
	9	11	63.6	2.0	1.49	10.3
	10	22	45.5	3.0	1.50	13.3
	11	4	25.0	0.2	2.00	0.7
1.8-3.7 km	12	23	95.7	7.9	1.25	41.7
	13	20	70.0	2.9	1.92	25.0
	14	19	73.7	2.4	0.94	8.3
	15	8	50.0	1.5	1.48	5.1
3.7-5.5 km	16	15	100.0	7.8	1.05	32.5
	17	26	73.1	2.6	1.55	20.0
	18	16	43.8	1.3	1.52	6.2
	19	3	0.0	0.0	—	0.0

Analysis of Variance:

Source	df	SS	MS	F	P
Total	312	401.42			
Area	18	206.37	11.46	4.74	0.01
Time (area)	47	62.30	1.33	2.46	0.01
Station (time (area))	247	132.76	0.54		

TABLE 6.—Ranking of food items by total abundance and frequency of occurrence, from 24 *Limulus polyphemus* collected in the Atlantic City series, summer 1978.

Item	Number of specimens	Rank	Number of occurrences	Rank
Foraminifera	136	1	9	5
Unidentified bivalve	65	2	13	2
Spisula	48	3	14	1
Tellina	42	4	10	4
Brachyura	16	5	11	3
Siliqua	16	5	6	6
Spionidae	15	6	3	9
Nematoda	10	7	4	8
Cancer	9	8	4	8
Fecal pellets	9	8	9	5
Plant material	9	8	9	5
Gemma	8	9	5	7
Glycera	7	10	3	9
Polychaete setae	6	11	6	6
Ensis	6	11	5	7
Polynoidae	6	11	3	9
Mytilus	4	12	4	8
Nereis	4	12	4	8
Cirripedia	3	13	3	9
Spiophanes	3	13	2	10
Ampharetidae	2	14	2	1
Anomia	2	14	2	10
Capitellidae	2	14	2	10
Isopoda	2	14	2	10
Mulinia	2	14	2	10
Nemertea	2	14	2	10
Ostracoda	2	14	2	10
Turbellaria	2	14	2	10
Unidentified gastropod	2	14	2	10
Unidentified oligochaete	2	14	1	11
(Tie-17 items)	1	15	1	11

noted in two samples and unidentified shells in three. The most numerous item was Foraminifera (n = 21), and no other item was found more than three times.

In a laboratory experiment, a 20.3 cm (prosomal width) male horseshoe crab ate one 40.6 mm surf clam; the same crab consumed two clams, 43.8 and 42.4 mm, several days later (see Botton 1982 for procedural details). A 27.9 cm female ate two clams, 46.0 and 36.2 mm. Clams of this size are manipulated by the walking legs so that the ventral shell margin is held against the gnathobases. The chitinous gnathobases chip the ventral margin, eventually resulting in the fracture of one of the valves. Cracking of the valves continues until the crab is able to remove the meat from the shell using the pincer-tipped walking legs or the chelicerae. Ingestion of the shell of 4 cm *S. solidissima* is apparently incidental.

DISCUSSION

A latitudinal gradient in horseshoe crab abundance along the New Jersey coast during the spring and summer months was recognized as a decrease in abundance with distance north from Delaware Bay, and an onshore-offshore gradient was apparent in northern New Jersey. The transition between areas of high and low density takes place between Great Egg Harbor Inlet (Ocean City) and Absecon Inlet (Atlantic City). Horseshoe crabs were more abundant inshore in the late spring and early summer than in the late summer and fall.

Why are adult *L. polyphemus* concentrated in southern New Jersey, at least during the spring and summer? Since Delaware Bay, in southern New Jersey, contains the largest spawning population of horseshoe crabs in North America (Shuster 1982), we believe that the distribution on the New Jersey continental shelf may be related to the migration of deep-water crabs to those beaches for reproduction. However, horseshoe crabs spawn elsewhere in New Jersey and are widely distributed on the middle Atlantic continental shelf (Shuster 1979); based on electrophoretic evidence (Selander et al. 1970), there is gene flow between widely separated populations.

Hydraulic surf clam dredges are efficient samplers of large benthic infauna (Meyer et al. 1981), but an evaluation of this dredge as a means of capturing *L. polyphemus* is lacking. Given its sluggish habits, it is unlikely that gear avoidance by horseshoe crabs significantly affects our results; indeed, much more active lady crabs, *Ovalipes ocellatus*, are caught in large numbers (Meyer et al. 1981; Haskin, unpubl. data). However, in the absence of direct observations, it is perhaps best to consider our results as relative, rather than absolute abundances of horseshoe crabs off New Jersey. Because the temporal sequence of sampling varied yearly and because the effect of time on abundance was statistically significant, we do not encourage speculation on year-to-year variability based on these data.

The horseshoe crab is a dietary generalist; based on the limited number of animals dissected, molluscs, arthropods, and polychaetes are the major food items. Although Foraminifera were numerous, they are probably ingested inadvertently while digging out infauna. Opportunistic foraging was shown from the Stone Harbor group, which fed almost exclusively on *M. edulis*. Smith (1953) noted that crabs could locate discrete patches of soft-shell clam, *Mya arenaria*, but the behavioral basis for patch selection is unknown.

Horseshoe crab predation may be an important source of juvenile surf clam mortality. In aquaria, crabs ingested only the meats of 4 cm *S. solidissima*; this implies that this species may be more important as food than is apparent from visual stomach content analysis, which relies heavily on shell remains. Young *S. solidissima* may have been underestimated because many small (0.5-2.0 mm) shells were categorized only as "unidentified bivalves." Further studies of the food habits of horseshoe crabs, and of the abundance and diets of other predators, are necessary to evaluate the importance of predation in the survivorship of juvenile surf clams in New Jersey.

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DIEL VARIATIONS IN THE FEEDING HABITS OF PACIFIC SALMON CAUGHT IN GILL NETS DURING A 24-HOUR PERIOD IN THE GULF OF ALASKA

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ABSTRACT

Changes in prey composition and stomach fullness indicate diel variations in feeding behavior of sockeye, pink, and coho salmon caught in surface gill nets set for 2 hours each over a 24-hour period at a station in the Gulf of Alaska. All of these species of salmon switched from feeding primarily on squids, fishes, and amphipods during the day to euphausiids at night. Apparently dense concentrations of euphausiids can be exploited by salmon in surface waters at very low light intensities, even during an overcast night. Day-night changes were less obvious in the food of chum salmon, which fed largely on salps. Total catches of salmon and catches in the near-surface portion of the gill nets were highest between sunset and sunrise, suggesting that diel vertical movements contribute to the higher night than day catches of surface gill nets.

Although many studies have been published on the feeding habits of salmonids in oceanic waters of the North Pacific Ocean (Andrievskaya 1957; Allen and Aron 1958; LeBrasseur 1966; Ito 1964; Manzer 1968; Takeuchi 1972), most studies of daily feeding patterns have been conducted on juvenile salmon in fresh water or in coastal waters. These have generally shown that juvenile pink, sockeye, and chum salmon are diurnal or crepuscular (dawn and dusk) feeders (see Godin 1981 for review). The few studies conducted on diel feeding variations of adult or maturing Pacific salmon in oceanic waters of the northwestern Pacific Ocean have not revealed a consistent pattern (Machidori 1968; Shimazaki and Mishima 1969; Ueno et al. 1969).

To further elucidate the diel feeding patterns of these fishes, we collected and examined stomach contents of four species of Pacific salmon caught in the Gulf of Alaska during one 24-h period.

METHODS

Two gill nets, each 800 m long and 6 m deep, with 300 m of 115 mm, 250 m of 121 mm, and 250 m of 130 mm (stretch) mesh, were alternately fished for about 2-h periods over a 24-h period in the Gulf of Alaska from the *Oshoro Maru*, training ship of the Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido. The first net was set at 1200 h local time (GMT - 9 h) on 13 July; the last set was hauled at 1206 h on 14 July 1981 (Table 1). The time that the gill nets were fishing varied in the first 11 sets from 140 to 152 min (from start of set to start of

TABLE 1.—Summary of gill net sets and catches for salmon, 13-14 July 1981.

Set no.	Start of set and haul (h)	Number of salmon					
		Sock-eye	Chum	Pink	Coho	Steel-head	Total
1	1200 1422	8	4	1	0	0	13
2	1400 1629	2	0	1	5	0	8
3	1600 1821	2	8	4	7	0	21
4	1800 2020	7	1	5	2	0	15
5	1957 2227	15	1	5	3	1	25
6	2158 0025	9	5	11	11	1	37
7	2359 0224	11	7	8	7	0	33
8	0159 0430	17	8	7	8	0	40
9	0358 0627	6	2	11	5	2	26
10	0600 0832	11	3	2	1	2	19
11	0758 1026	7	1	6	1	0	15
12	0957 1206	12	4	7	1	0	24
	Total	107	44	68	51	6	276

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hauling) and 129 min in the last set. Five to eight minutes were required to set the nets, 12-20 min to retrieve them.

The study area was between lat. 54°51.5′ and 54°57.9′N, long. 144°55.1′ and 145°11.3′W. On consecutive sets the gill nets were set 1.5-30 km apart to reduce the possibility of one net influencing the catch of another. Gill nets were set along a ship course of 040°, except for the first two nets which were set along 230°. In general, nets drifted 0.4-6.5 km northeastward during the sets.

The vertical location in the gill net (upper, middle, and lower 2 m) and species of each captured salmon were noted as the gill net was hauled aboard. Fish were removed from the gill nets, measured (fork length), and weighed with a beam balance. Stomachs were removed, weighed to the nearest gram with a beam balance, placed in a tray, and cut open with scissors. The fullness of cardiac and pyloric portions of the stomach was estimated visually as a) empty, b) trace amounts (few individual organisms with cumulative weights of a gram or less), c) <⅓ full, d) ⅓-⅔ full, and e) full (rugae fully distended, stomach lining thin and translucent). The degree of digestion was estimated as a) fresh (prey intact, no obvious digestion; fishes and squids with intact skin, euphausiids translucent), b) partially digested (fishes and squids identifiable, their skin, but not flesh, largely digested; euphausiids opaque, appendages often absent), and c) digested (fishes consisting of pieces of white flesh and vertebrae, crustaceans in pieces, euphausiids sometimes identifiable from fragments, especially their eyes).

The percentage composition by volume of prey taxa (euphausiids, amphipods, squids, fishes, salps, pteropods, copepods) was visually estimated for the cardiac and pyloric portions of each stomach. Stratification of food taxa in the cardiac portion was noted. Stomachs with diverse prey taxa were flushed into a petri dish to facilitate identification and estimation of prey compositions. Samples of prey organisms were preserved in Formalin[4] for verification and identification to lower taxa. Stomachs with more than trace amounts of food were then rinsed with water to remove adhering food items, blotted, and reweighed to the nearest gram.

The data were all obtained during the 2-h periods after setting one gill net and hauling the other.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Catches of Salmon

A total of 107 sockeye, 68 pink, 51 coho, and 44 chum salmon and 6 steelhead trout were caught in the 12 sets (Table 1). In general, the catches of each species were highest between sunset (2113 h) and sunrise (0420 h). This trend is clearly shown in Table 1. Catches were several times larger during night sets (1957-0627 h, sets 5-9) than sets that fished during daylight periods.

To illustrate diel trends in the vertical distribution of the salmon captured in the gill net, catches of a species were combined (because of the low numbers of individual species caught per set in each vertical section of the net) for afternoon (sets 1-5), night (sets 6-8), and morning (sets 9-12). Figure 1 shows that the average percentage of all species of salmon caught in the upper 2 m of the gill net was highest at night. Moreover, as the lower part of Figure 1 illustrates, peak catches of all species combined occurred at night.

Length-frequency distributions of the four species of salmon from the catches at all sets combined are shown in Figure 2. Fish of several ocean

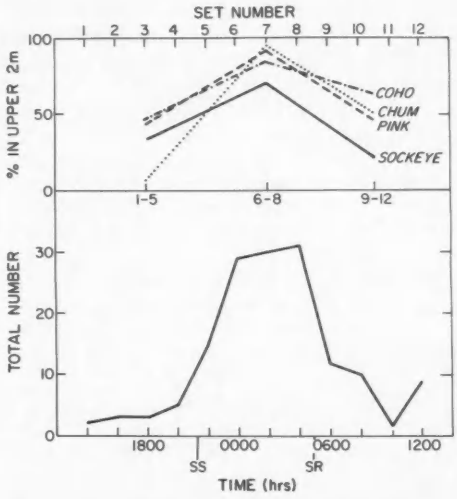

FIGURE 1.—Average percent of the total catch of the four species of salmon caught in the upper 2 m of the gill net during afternoon (sets 1-5), nighttime (sets 6-8), and morning hours (sets 9-12) (upper panel), and the total number of all species of salmon caught in the upper 2 m of the gill nets per set during the 24-h period (lower panel).

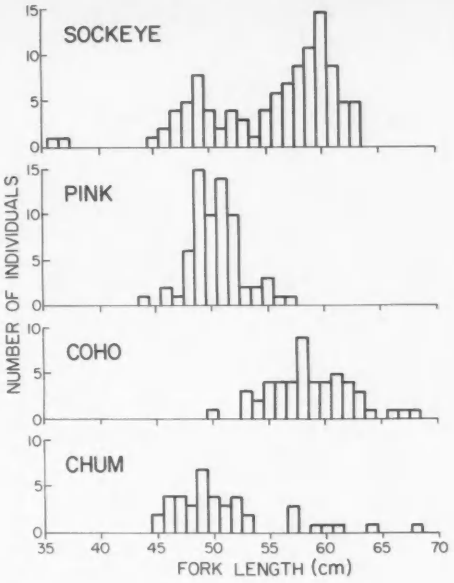

FIGURE 2.—Length-frequency histograms for the four species of salmon caught in the 24-h study.

ages are represented for sockeye and chum salmon. All pink and coho salmon were probably beginning their second year of ocean life. Comparisons of length-frequencies between day (sets 1-4 and 10-12) and twilight and night (sets 5-9) were not significantly different for sockeye, pink, and chum salmon, but were significant for coho salmon (Kolmogorov-Smirnov test, $P < 0.05$). Coho salmon were 2.4 cm larger in the twilight-night sets.

Feeding Habits

Stomach fullness of the four species of salmon, calculated as a percentage of body weight, were usually variable, ranging from 0% (empty) to a maximum of 4% for sockeye, 3.0% for chum, 3.3% for coho, and 2.3% for pink salmon (Fig. 3). Some individuals of all species had empty stomachs during most sets, regardless of time of day. Although ranked differences of the stomach weight:fish weight ratio were not significantly different between day (sets 1-4 and 10-12) and night-twilight (sets 5-9) for each of the four species of salmon (Mann-Whitney U-test, $P > 0.05$), the highest percentages of stomach weight to body weight for sockeye (>3%) and coho and pink salmon (>2%) were obtained from nighttime sets (Fig. 3). Moreover, our visual estimates of stomachs also indicated that full, distended stomachs of sockeye, coho, and pink salmon occurred only at night. There were no suggestions of diel periodicity of stomach fullness for chum salmon, however.

The frequency of occurrence and percent composition of the most common prey taxa (euphausiids, amphipods, squids, fishes) in the cardiac portions of salmon stomachs containing more than trace amounts of food are summarized in Table 2. All species of salmon consumed all of the four major categories of food. The most frequently occurring major taxa was euphausiids in sockeye and coho salmon, amphipods in pink salmon, and "other taxa" (mainly salps, but often unidentified material and sometimes pteropods and polychaetes) in chum salmon stomachs. Amphipods were the second most frequent taxa in

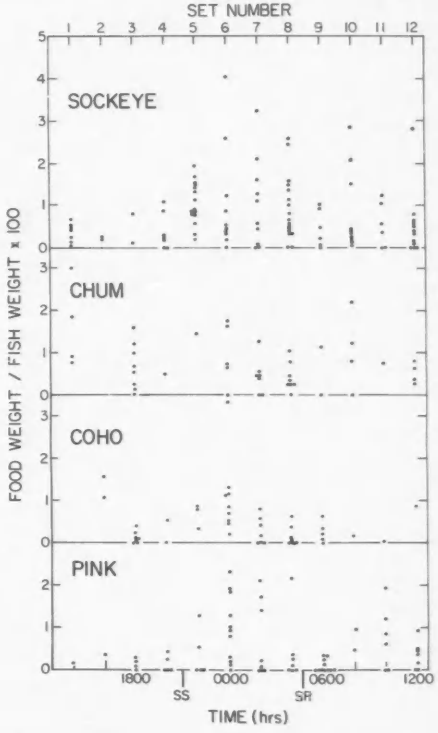

FIGURE 3.—Stomach fullness, expressed as a ratio of food weight to fish weight, for the four species of salmon caught in each of the 12 gill net sets during the 24-h period.

TABLE 2.—Frequency of occurrence and mean percent composition of major prey taxa in the gastric portions of salmon stomachs containing more than trace amounts of food.

		% occurrence					% volume				
	No. of stomachs	Euphausiids	Amphipods	Squids	Fishes	Other	Euphausiids	Amphipods	Squids	Fishes	Other
Sockeye	92	73	40	17	18	17	53	18	9	14	5
Pink	35	49	63	17	17	11	37	35	9	14	4
Chum	27	41	37	4	7	78	29	10	2	4	56
Coho	30	63	33	43	3	0	54	3	39	4	0

sockeye, euphausiids in pink and chum salmon, and squids in coho salmon stomachs.

The same taxa that ranked first and second on a frequency of occurrence basis usually ranked first and second on the basis of mean percent volume. Euphausiids (mainly *Euphausia pacifica* and *Thysanoessa longipes*) were most important for sockeye, pink, and coho salmon; "other taxa" were most important for chum salmon. Amphipods (mainly *Parathemisto pacifica* and *Hyperia medusarum*) ranked second in sockeye and pink salmon. Gonatid squids ranked second in coho stomachs and euphausiids ranked second in chum salmon stomachs. Thus sockeye fed primarily on euphausiids and secondarily on amphipods and myctophid fishes. Pink salmon fed mostly on euphausiids and amphipods. Coho fed mainly on euphausiids and squids, and chum on salps and euphausiids (see Table 2). Squids comprised only 2% of the volume of the stomach contents of chum salmon, and fishes comprised only 4% of the volume for chum and coho salmon. Copepods were not important (<1% of volume) for any species of salmon captured during the study.

Dietary overlap, based on the sum of minimum percentage volumes (percent similarity index, PSI, Sanders 1960) of the four main prey taxa, was 78% between sockeye and pink, 69% between sockeye and coho, and 53% between pink and coho. Because chum salmon had the most unique diet of the four species consuming mainly salps and gelatinous zooplankton, they had overlap values of only 45% with sockeye and pink and 38% with coho.

Although all species of salmon fed on a variety of taxa, individual fish usually contained only a few prey taxa. Only two major prey taxa were found in 85%, 89%, 93%, and 89% of the cardiac portions of sockeye, pink, coho, and chum salmon stomachs, respectively, containing more than trace amounts of food. Most sockeye and pink salmon had only one taxon of food in their stomachs. When salmon had only one food type in their stomachs, it was euphausiids in 65%, 52%, 85%, and 28% of the individual sockeye, pink, coho, and chum salmon, respectively. Euphausiids were obviously the most important prey for sockeye, pink, and coho salmon during this study. They were often the exclusive prey.

Sometimes the contents of the cardiac portion of sockeye and pink salmon stomachs were clearly divided with one type of prey in the anterior and one in posterior portion of the stomach. Generally this "stratification" involved euphausiids and amphipods, or euphausiids and squid. Usually, however, the cardiac and pyloric portions of the stomach had similar percentage compositions of major taxa (excluding empty stomachs and stomachs with trace amounts). Cardiac and pyloric contents were similar for 70% of the sockeye, 72% of the pink, and 60% of the coho and chum salmon. When sockeye and coho had the same prey composition in cardiac and pyloric stomachs, both portions usually contained only euphausiids. When pink salmon had the same prey composition, amphipods or euphausiids were found.

The relative composition of major prey taxa in the stomachs of each species caught in the 12 gill net sets is illustrated in Figure 4 and is discussed below. Open circles in Figure 4 indicate when fresh prey were common, except for amphipods which usually showed little evidence of being digested.

Sockeye Salmon

Prey composition of sockeye salmon had a distinctive diel pattern. Sockeye caught at night (2158-0430 h) contained a high percentage of euphausiids compared with the afternoon and morning sets (Fig. 4). In these night sets, euphausiids averaged over 80% of the volume of the stomach contents, and about 90% of the sockeye contained only euphausiids. Fish caught during and after sunset (1957-0224 h) also contained large numbers of freshly ingested euphausiids. Some fish in set 5 (1957-2227 h) had a clear division between euphausiids in the fore portion and amphipods in the posterior portion of the cardiac

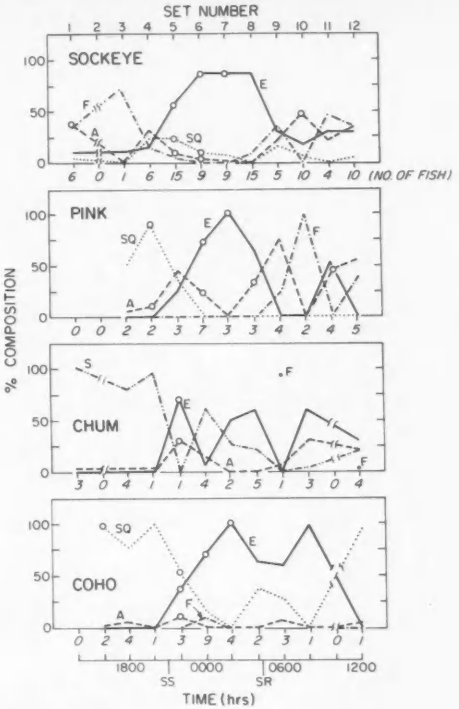

FIGURE 4.—Diel variations in the percent composition of major prey taxa in the stomachs of the four species of salmon containing more than trace amounts of food. E = euphausiids, A = amphipods, F = fishes, SQ = squids, S = salps. Open symbols show when fresh prey was common. The number under each figure indicate the number of fish with more than trace amounts of food in their stomachs. SS = sunset; SR = sunrise.

stomach, indicating a switch from amphipods to euphausiids during dusk. Euphausiids comprised <30% of the food in sets before sunset and after sunrise, and no fresh euphausiids were noted during these daytime periods. Amphipods and fishes formed the highest percentage of the food during daytime. Squids were also eaten by sockeye salmon and were most important during late afternoon and sunset (1800-2227 h) and during sunrise (0350-0627 h). Fresh squids were noted in stomachs of fish caught in sets that fished from 1957 to 0025 h.

Pink Salmon

As with sockeye salmon, euphausiids attained peak importance as prey for pink salmon after sunset (2158-0430 h), when they comprised over 65% of the food and were often in fresh condition. All three fish with over trace amounts of food in the set that fished from 2359 to 0224 h contained 100% euphausiids. Squids and amphipods are most important in the afternoon (1600-2020 h), and fresh squids were found in stomachs of pink salmon caught from 1800 to 2020 h, just before sunset. Fishes and amphipods were the most important prey during the morning daylight period.

Chum Salmon

A diel trend for this species, which fed on a variety of prey taxa, was less obvious than for other species of salmon (Fig. 4). Salps composed over 75% of the stomach contents during the afternoon (1200-2020 h). Euphausiids were the most common prey taxa from sunset to the last set at midday, with the exception of a single chum salmon caught at 2158-0025 h whose stomach contained many salps and a salmon caught at 0358-0627 h whose stomach contained 95% fish. Most euphausiids in the stomachs of fish caught about the time of sunset (1957-2227 h) appeared to be recently ingested. Squids, which were only a minor part of the stomach contents, are not indicated in Figure 4.

Coho Salmon

Coho salmon fed mainly on euphausiids during the night and on squids during the day. Euphausiids were not observed in stomachs of coho salmon during the afternoon but increased in importance from 0 to 100% of the stomach volumes between 1800 and 0240 h (Fig. 4). Most of the euphausiids during this period were in fresh condition. Euphausiids also comprised most (>60%) of the stomach contents during the morning hours (0159-0832 h) but were never fresh. Squids were the most important prey of coho salmon caught during the afternoon-daylight period and in the last set in late morning. Amphipods and fishes were of minor importance.

DISCUSSION

The larger catches of salmon in surface gill nets during twilight-night periods than in daytime periods have three possible explanations: Avoidance of nets during the daytime when visual acuity of salmon is highest, increased swimming

activity in surface water at night compared with daytime, and diel vertical ascent of salmon into near-surface waters at night. The higher catches in the upper 2 m of the gill net at night than day lend support to the last possibility, but not to the exclusion of the other possibilities.

Most other authors favor vertical migration as an explanation for diel peaks in gill net catches (Taguchi 1963; Manzer 1964; Mishima et al. 1966). Birman (1964) noted visual avoidance of "sweep nets" by day, but concluded that salmon migrate into upper waters primarily as a response to vertical movements of their zooplanktonic prey which they feed on during periods of low light intensity, chiefly before dawn.

Swimming activity could also influence catchability, but neither Ichihara et al. (1975) nor Ichihara and Nakamura (1982) found large differences in day-night swimming speeds of chum salmon tagged with ultrasonic transmitters.

The most interesting finding of our study is the distinct diel change in composition of major prey. Stomach contents of sockeye, pink, and coho salmon were comprised largely of euphausiids after sunset and during the night (Fig. 4). The largest number of full stomachs, usually containing only fresh euphausiids, were also found during the nighttime. These three species of salmon preyed intensively on euphausiids at night, often to the exclusion of other types of prey.

This change to feeding on euphausiids was first observed in the salmon caught during the time that the 24-kHz sonic scattering layer ascended into surface waters (Fig. 5). We assume that euphausiids were an important component of this scattering layer (see Suzuki and Ito 1967).

A 1.8 m Isaacs-Kidd midwater trawl collection (three mesh sizes: 70, 11, and 4 mm stretch) in the upper 10 m at night at the 24-h gill net station caught mainly salps and medusae, but euphausiids were abundant (19g/1,000 m^3). Euphausiids were also abundant in a 1.3 m ring net (1.0 mm mesh) towed at the surface after sunset at this station. The most common euphausiids caught were *Euphausia pacifica* and *Thysanoessa longipes*, the same species common in salmon stomachs. *Euphausia pacifica* were found to undertake diel vertical migrations at the Canadian Weather Station located at lat. 50°N, long. 145°W (Marlowe and Miller 1975). Frost and McCrone (1974) also found evidence for diel vertical migration of *E. pacifica* at this location but not for *T. longipes*. The intense predation on euphausiids at night is therefore thought to be related to their dense concentration and increased vulnerability in surface waters after dark.

Most of the studies of the diel periodicity or chronology of feeding in salmon have been juveniles in fresh or coastal waters (Godin 1981). In general, these indicate diurnal or crepuscular feeding patterns for juveniles of pink salmon (Ali 1959; LeBrasseur and Barner 1964; Bailey et al. 1975; Parker and Vanstone 1966; Parker 1969; Godin 1981), chum salmon (Bailey et al. 1975; M. C. Healey as cited in Godin 1981), sockeye (Narver 1970; McDonald 1973; Doble and Eggers 1978), and coho salmon (Mundie 1971). Bailey et al. (1975) concluded that pink and chum salmon fry did not feed during cloudy moonless nights. Nighttime feeding by sockeye apparently occurs during moonlight but not on cloudy or moonless nights in Babine Lake (Narver 1970). Experiments conducted by Brett and Groot (1963) and Ali (1959) indicated that juvenile pink salmon changed their mode of capturing prey below 10^0 mc (meter candle), an intensity where the change from phototopic to scotopic vision apparently occurs, and their feeding activity decreased between intensities of 10^0 to 10^{-4} mc and most ceased between 10^{-3} and 10^{-5} mc. Experiments by Bailey et al. (1975) showed almost no feeding by pink salmon fry at light intensities below 10^1 mc.

In our study, salmon fed intensively on euphausiids at night under an obscured, overcast sky. From the general data given by Brown (1952) and Blaxter (1970) we estimated that the light intensities on this night were between 10^{-3} and about 10^{-5} mc. But, despite these low light intensities, with attendant reduction in contrast of prey and sighting range to prey (Eggers 1977; Anthony 1981), salmon were capable of actively feeding on small, euphausiid-sized prey. At night, larger prey such as squids and fishes are probably encountered less frequently than euphausiids and evade capture more easily because of reduced sighting and tracking ranges of salmon. Euphausiids may not be as capable of active predator evasion and, when abundant in near-surface aggregations at night, are encountered frequently and actively selected. Bioluminescense produced by euphausiids may facilitate detection and capture by salmon. Thus, escape responses and sighting ranges at different light intensities may influence the size and type of prey selected at different times of a diel period.

Machidori (1968) reported that the indices of stomach:body weight of sockeye and chum salmon caught in gill nets that fished different depths

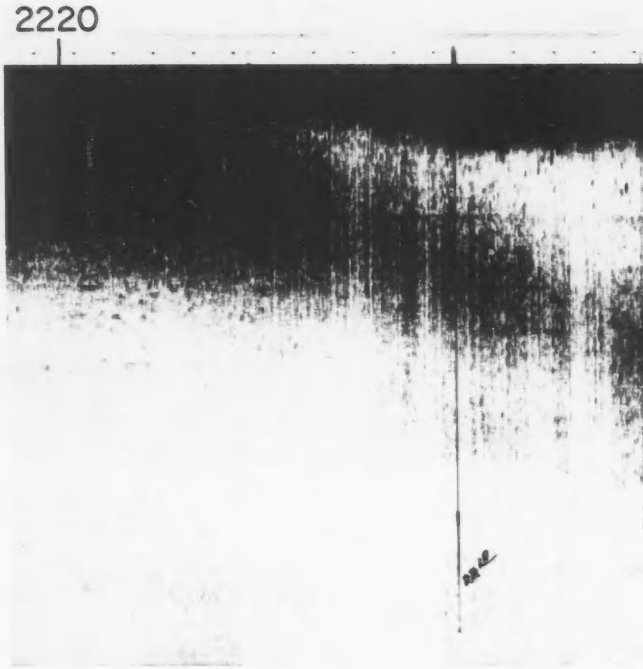

FIGURE 5.—24-kHz echogram from 2150 to 2220 h on 13 July 1981 sh

1981 showing the ascent of a sonic scattering layer into near-surface waters.

between 0 and 50 m in the northwestern Pacific were usually highest in near-surface depths by day and below 10 m at night. Euphausiids were an important food taxa only in salmon caught below 10 m during the day. Since average stomach fullness indices were higher during the day than the night, Machidori concluded that light was necessary for salmon to feed. Takagi (1971) reported that surface longlines and gill nets caught salmon during morning and evening, but during the night salmon were caught in gill nets but not by longlines. These observations indicate reduced feeding activity of salmon at night.

Shimazaki and Mishima (1969) concluded from diel trends in the feeding of maturing pink and chum salmon at two locations in the Sea of Okhotsk that feeding activity was high in the evening before and after sunset and low in daytime. They found peak stomach fullness values after sunset. In three of four instances these peak values were the first values after sunset, and may have been the result of crepuscular feeding. In one instance involving pink salmon, however, stomach fullness increased from 1917-2040 h to a peak at 2119-2245 h, indicating active feeding at night. Amphipods, squids, and fishes were the dominant food on a wet weight basis.

Additionally, Ueno et al. (1969) found that pink and chum salmon had full stomachs during the late afternoon as well as after dark in waters off Kamchatka. Suzuki (1970) compared the volume of food in stomachs of chum salmon caught in gill nets off the Kamchatka Peninsula during night (2100-2330 h) and morning daylight hours (0330-0610 h) and concluded that no major differences existed. He found that myctophid fishes always comprised a larger percentage of the stomach contents during the morning and pteropods usually comprised a larger percentage at night.

Thus the above studies plus our own clearly document that salmon are capable of feeding during both day and night periods in oceanic waters. Their feeding behavior is flexible and variable, permitting opportunistic exploitation of a profitable food resource regardless of when it is encountered.

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ARCTIC CHAR PREDATION ON SOCKEYE SALMON SMOLTS AT LITTLE TOGIAK RIVER, ALASKA[1]

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ABSTRACT

Observations of Arctic char feeding on migrating sockeye salmon smolts at Little Togiak River, Alaska, indicate a Type II functional response where the number of smolts consumed increased with smolt abundance. The number of smolts migrating was usually low (<20,000 smolts/24 hours) and the corresponding consumption of smolts averaged 0.8 smolts/char per 24 hours. When large smolt migrations occurred (>80,000 smolts/24 hours), char consumption of smolts generally increased to 5.6 smolts/char per 24 hours. In addition to smolt abundance, smaller smolts and longer char were correlated with an increase in the number of smolts consumed. Estimates of percent smolt mortality, based on two hypothetical char numerical responses to varying smolt abundances, indicate that smolts were migrating at densities most susceptible to predation.

A comparison of length of smolts consumed by char with those in the migration shows that char consumed larger than average smolts when their stomachs were not full and smaller than average smolts when char approached stomach fullness. This may be explained by the migration of larger smolts during the feeding period of char and the possibility of char feeding less effectively when approaching fullness. Although major hatchery releases often exceed 100,000 smolts per day, these data suggest that hatchery-released smolts may be less susceptible to predation in small rivers when released during the night in large numbers (>20,000 smolts/24 hours).

The relationship between predation on juvenile salmon and relevant biological and environmental factors is important to the understanding of salmon population dynamics. Development of these relationships may be useful for establishment of "optimal" escapement levels and for maximum production from salmon enhancement projects. A few investigations have related predation rates to juvenile salmon abundance and have reported up to 85% juvenile mortality (Neave 1953; Hunter 1959; Parker 1968; Peterman and Gatto 1978). Other investigations have examined the effect of biological or environmental variables such as juvenile salmon size (Parker 1971), predator size (Ricker 1941; Hunter 1959; Rogers et al. 1972), infection by parasites (Burke 1978), river velocity and turbidity (Ginetz and Larkin 1976), thermal stress (Sylvester 1972; Coutant 1973), or several variables independent of juvenile salmon density (Fresh et al. 1980). No investigation has analyzed predation while concurrently assessing the partial effect of prey density along with the partial effect of biological and environmental factors.

This investigation represents a 5-yr study of predation by Arctic char, *Salvelinus alpinus*, on emigrating sockeye salmon, *Oncorhynchus nerka*, smolts at Little Togiak River, Alaska (Fig. 1). Predator-prey interaction appears to be especially refined in this river. With the onset of the smolt emigration each spring, char migrate to the interconnecting rivers in the lake system where migrating smolts are most vulnerable (McBride 1979). After the smolt migration ends, char return to their spawning streams in the fall. The objectives of this investigation, which were tested during this brief period of predator-prey interaction, were 1) to empirically model the daily functional response of char (i.e., the relationship between smolt abundance and number of smolts consumed/char per 24-h period (Fig. 2)) while concurrently measuring the effect of biological and environmental variables; 2) to estimate percent smolt mortality in relation to smolt abundance; and 3) to test for disproportional consumption of large or small smolts by char that differ in stomach fullness and fork length.

Numerous biological and environmental variables are likely to influence char predation on salmon smolts. The variables concurrently tested in the functional response model were 1) the number of migrating smolts during the 24-h period prior to sampling the char; 2) the number of migrating smolts during the 24-48 h period prior to sampling; 3) smolt weight; 4) char length; 5)

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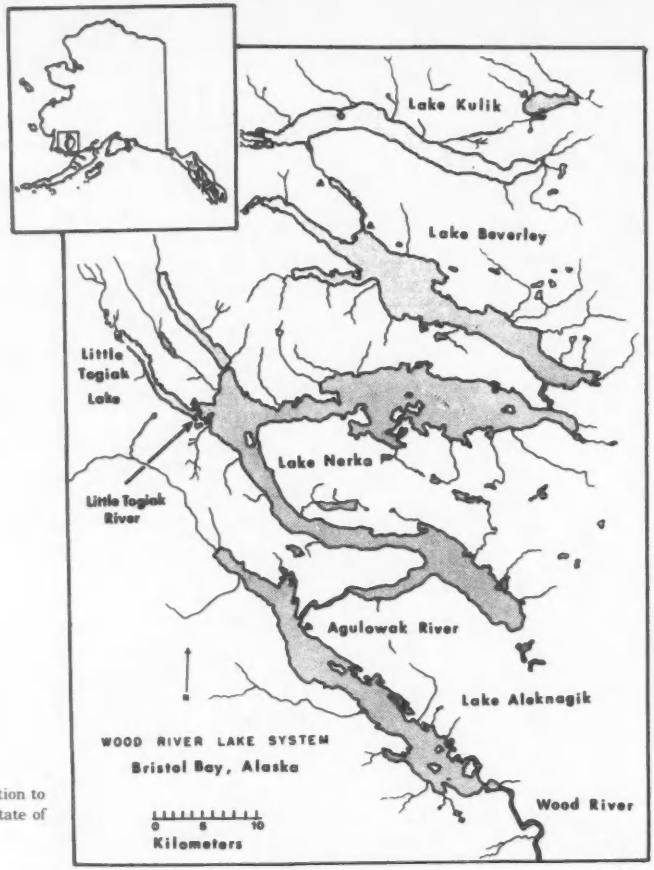

FIGURE 1.—Little Togiak River in relation to the Wood River lake system and the State of Alaska.

number of smolts migrating during the daylight; 6) percent of migration during the daylight; 7) presence of adult sockeye in the river; 8) days after ice-out; 9) river temperature; 10) river depth; 11) light intensity at dusk; and 12) incident solar radiation.

METHODS

Description of Study Site

Little Togiak River is a small nonturbid river located in the Wood River lakes system, Alaska (Fig. 1). River length is about 200 m as it flows from the smaller Little Togiak Lake to the larger Lake Nerka. River width is about 20 m and average depth ranges from about 2 m during spring high water to <1 m during midsummer.

Collection of Char Samples

Arctic char were collected from Little Togiak River from 1976 to 1980. Each year the sampling season began soon after ice breakup (about 7 June) and terminated at the end of the smolt migration near the end of July. About 10 char were collected daily during the morning and/or the evening (shortly before and after the peak smolt migration), and their stomach contents were analyzed within 1 h after capture. Information on the size of smolts consumed and on the population size of char at Little Togiak River was collected only in 1980.

Char were collected by fishing with unbaited

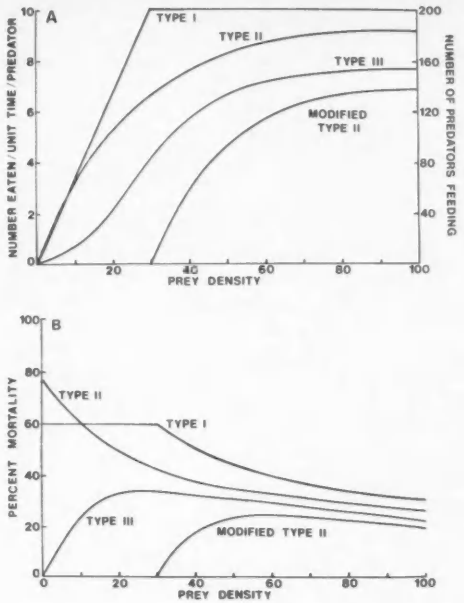

FIGURE 2.—Shapes of different types of hypothetical functional (left ordinate) and numerical responses (right ordinate) (A) and percent mortality curves (B) (redrawn from Holling 1959; Peterman and Gatto 1978).

lures from 1976 to 1979. In 1980, the primary method of char capture was a variable mesh size (5.1, 6.4, 7.6, and 10.2 cm stretch measure), monofilament gill net set across the river and allowed to drift downstream for 15 min. Nonparametic statistical analysis of 99 char caught by hook and line or gill net on the same day indicated no significant difference in char consumption of smolts estimated by each method (Mann-Whitney U-test: $0.10 < P < 0.20$). The collected char were anesthetized with tricaine methane sulfonate (MS-222), then their stomach contents were flushed out by a stomach pump. Examination of stomach contents from sacrificed char showed that about 90% of the smolts were removed by the pump. Before returning the char to the river, we measured the fork length and placed a numbered Dennison flag-type tag just below the dorsal fin. Stomach fullness was estimated visually and categorized as either full or less full.

Consumed Smolt Analysis

Smolts consumed by char were counted and measured after standardizing their length in 10% Formalin[3] for at least 24 h (Burgner 1962). The consumed smolts were measured by one of three methods and converted to fork length using one of the following regression equations (Ruggerone 1981):

1) Fork length (mm) = 0.44 + 1.09 (standard length); $r^2 = 0.99$;
2) Fork length (mm) = 3.70 + 1.37 (pectoral fin to hypural bone plate); $r^2 = 0.98$.

The preferred method of measurement was fork length; the next preferred method was standard length. When neither of these methods was adequate, the length from the pectoral fin insertion to the hypural bone plate was measured. Preserved fork length measurements were multiplied by a factor of 1.042 to convert back to "live" fork lengths (Rogers 1964).

Collection and Enumeration of Migrating Smolts

Migrating smolts were collected and enumerated with a winged-fyke net placed in an area of intermediate, but substantial water flow. Smolts trapped in the "live box" were counted and set free every 4 h during the day (0800-2200 h) and continuously during the major migration period (2200-0200 h). Daily smolt abundance was estimated by multiplying the fyke net counts by a river width factor. Previous experimentation with two fyke nets indicated an even distribution of smolts across the river. At least one sample containing 30 or more smolts was collected each night for length measurements, and when a substantial number of smolts migrated during the day, an additional sample was collected. Samples to determine a length-weight relationship were collected about every 10 d. Fork lengths were measured to the nearest mm and weights to the nearest 0.01 g.

Environmental Data Collection

The water temperature of Little Togiak River was measured to the nearest 0.1°C several times each day. To account for smolt density in the water column, we measured the water level of Lake Nerka as an approximation of the relative water depth in Little Togiak River. The water level was

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

measured continuously with a lake level recorder and calibrated every 2 wk with benchmark measurements in Lake Nerka. To measure the effect of light on the feeding success of char, we measured incident solar radiation continuously with a pyrheliometer. As a qualitative measure of light intensity after sunset, we used a scale from 0 to 4 where 0 represented clear skies with relatively high light intensity and 4 represented low overcast skies with relatively low light intensity.

Data Analysis Procedures

Functional Response of Char

To determine the functional response of char and the effects of other variables on the number of consumed smolts, we grouped the data into 24-h periods with 1200 h as the first hour of the day. The number of smolts consumed per 24 h by an individual char was calculated by the following equation:

$$N = S\left(\frac{24}{D}\right),$$

where N = number of smolts consumed/char per 24 h
S = number of smolts observed in a char stomach
D = digestion time.

Average digestion time (h) was determined from data collected by Meacham and Clark (1979) and calculated by the following curvilinear equation (Fänge and Grove 1979):

$$\ln D = 4.892 - 0.143\,(T),$$

where D = digestion time
T = temperature (°C).

The functional response model based on multiple regression analysis was developed with the SPSS nonlinear program utilizing Marquardt's method of least squares estimation (Marquardt 1963). Residual and partial residual analysis were used to determine which independent variables should be added and the shape of their partial effect curve (Larsen and McCleary 1972; Draper and Smith 1981). This method allows for analysis of each new variable while including the effect of previous variables.

Percent Smolt Mortality

The average number of smolts consumed per char, as described by the functional response, may not represent the entire char population. Char may migrate to the river to feed, then return to the nearby lake environment for several days. Evidence for this behavior stems from gill net catches of char along the nearby lake shore and several underwater observations of relatively few char in the river during midday. Because the numerical response of char is not known, 2% mortality curves were developed from two hypothetical responses. The first percent-mortality curve was based on the assumption that the entire char population of 1,100 fish (Ruggerone 1981) fed each day (Type I numerical response; Fig. 2A). The second curve was based on the assumption that char immigrate to the feeding area in response to smolt abundance, thus a Type II numerical response was assumed (Fig. 2A).

Char Consumption of Smolts by Length

A two-factor analysis of variance with replication (Zar 1974) was used to test for random consumption of smolts by char. We divided the char data into three time periods containing two levels of char stomach fullness (full or less full) and three sublevels of char length (295-445 mm; 446-470 mm; 471-502 mm). To concurrently compare the length of smolts consumed by char with those smolt lengths available in the migration, we calculated the difference between average length of smolts consumed and average length of smolts available. This difference was utilized in each level of analysis.

RESULTS

Char Functional Response

Nonlinear regression analysis indicated that 4 of the 12 variables tested affect the number of smolts consumed/char per 24 h. The most important of these variables was the number of smolts migrating during the previous day's migration (approximate partial F, $P < 0.01$). The next important variable was the average weight of migrating smolts ($P < 0.01$), then the number of smolts migrating during the day of capture ($P < 0.01$), and finally char length ($P \leq 0.08$). The amount of variability explained by all four variables was 59% and the standard deviation was ±0.8 smolts

consumed/char per 24 h. Other variables such as the number of smolts migrating during the daylight, the percent of smolts migrating during the daylight, the presence of adult sockeye, days after ice-out, river temperature, incident solar radiation, light intensity during the evening as a function of cloud cover, and river depth as a function of lake level did not add any new information.

The model describing char consumption of smolts has the following form:

$$N = a + b(1 - e^{-cP}) + de^{-W} + f(1 - e^{-gC}) + hL^{3.02}$$

where a, b, c, d, f, g, h = empirical constants
N = number of smolts consumed/char per 24 h
P = number of smolts during previous migration
W = smolt weight
C = number of smolts during day of capture migration
L = char length.

A graphical interpretation of the empirically derived model is shown in Figure 3. Confidence intervals about each curve are difficult to interpret because they do not consider the concurrent value of other parameters (Draper and Smith 1981) and are not shown. Instead, a plot of smolts consumed by char versus the number of smolts migrating in the previous day's migration demonstrates the initial variability and the basis for the model (Fig. 4). The average predicted consumption rate was 0.8 smolts/char per 24 h and the maximum was 5.6 smolts/char per 24 h. These predictions were similar to the observed average and maximum consumption rates of 0.8 and 6.0 smolts/char per 24 h.

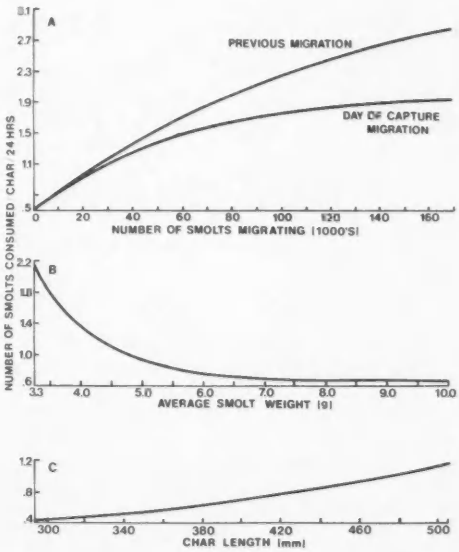

FIGURE 3.—The partial effect of the previous day's migration, the day of capture migration (A), average smolt weight (B), and Arctic char fork length (C) on the number of smolts consumed/char per 24 h. Smolt consumption was calculated by setting the alternate variables to their mean value.

The functional response of char was best described as a Type II response and was separated into two curves: consumption of smolts versus smolt abundance during the day of char capture and consumption of smolts versus smolt abundance during the previous day (Fig. 3A). Two curves were needed because most char digestion times were longer than 24 h. Thus, the predicted number of smolts consumed/char per 24 h was an average based on 2 successive days of feeding. The maximum partial effect of smolt abundance on the char consumption rate was about 3.7 smolts/char per 24 h when other variables were held at their mean values.

Smaller smolts and larger char were associated with increased consumption rates by char. Consumption of smolts increased exponentially with

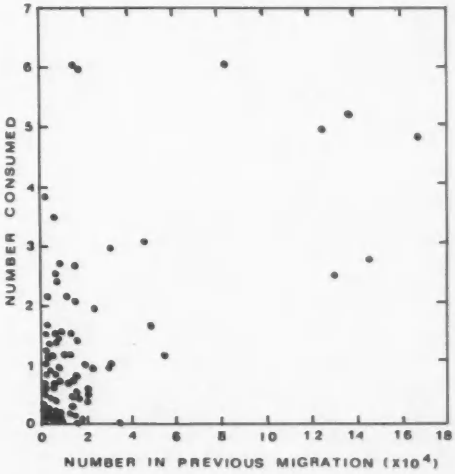

FIGURE 4.—Smolt consumption/Arctic char per 24 h in comparison with smolt abundance during the previous day's migration.

lighter smolts and increased curvilinearly with longer char (Fig. 3B, C). The maximum increase in char consumption of smolts due to changes in smolt weight and char length was about 1.4 and 0.8 smolts/char per 24 h, respectively.

The predicting power of this model is weak at high consumption rates by char. This problem arises from increasing residual variability as the predicted value increases. Increasing residual variability is usually corrected by using a weighting factor; however, when applied, the only data points carrying weight were those near the origin and any relationship between the variables was lost. Linear models were attempted, but did not approach the fit of the nonlinear model. Thus, at high rates of consumption by char, the model is best used for descriptive purposes.

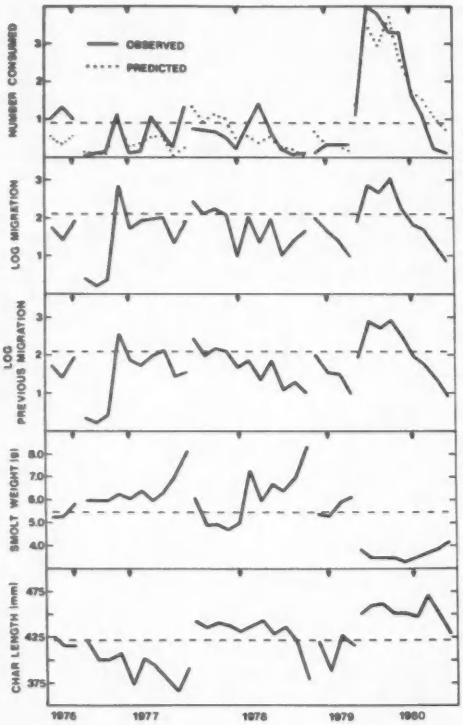

FIGURE 5.—Comparison of observed and predicted smolt consumption/Arctic char per 24 h with smolt abundance, average smolt weight, and char length during each sampling year. Data grouped into 3- to 5-d sampling periods. Dash line indicates mean value for all years. Log smolt abundance calculated from hundreds of smolts migrating. Arrows indicate entry of adult sockeye salmon in to Little Togiak River.

Comparison of consumption rates by char between years demonstrates the large variability that may be explained by smolt abundance, smolt weight, and char length (Fig. 5). During 1980 there were more than three times the number of migrating smolts, the weight of smolts was 30-50% less, and length of char was 24-68 mm greater than in any of the previous years. The combined effects of these variables resulted in a relatively large number of consumed smolts per char, which was also predicted by the model.

Percent Smolt Mortality

Two different percent smolt mortality curve types were produced from the two hypothetical numerical responses (number feeding) and the estimated consumption rates of char. A Type II curve (Fig. 2B) exhibiting an inverse relationship between percent smolt mortality and smolt abundance was produced from the assumption that all 1,100 char fed each day (Fig. 6A). Smolt mortality ranged from 0 to 100% when the number of migrating smolts was $<$ 6,750 smolts/24 h and $<$15% when the number of migrating smolts exceeded 20,000 smolts/24 h. A Type III percent mortality curve was produced from the assumption that the number of char feeding varied with smolt abundance (Fig. 6B). Although variability exists, percent mortality increased at low smolt abundances ($<$20,000 smolts/24 h), then decreased after char became overwhelmed and/or satiated[4] by smolts.

Char Consumption of Smolts by Length

The comparison of mean lengths of smolt consumed by char with mean length in the migration indicates that less full char consumed larger than average smolts ($\bar{d}$ = 1.7-2.9 mm, α = 0.05; Fig. 7). Char with full stomachs consumed smolts that were not different than the average length in the migration ($\bar{d}$ = −0.1-0.6 mm, α = 0.05). The length of char did not have a significant effect on the length of smolt consumed.

The comparison of length of smolts consumed in each stomach fullness category with the length

[4]During days of large smolt migrations, the number of smolts observed in individual char ranged from 0 to 45 smolts (not corrected by digestion period). Because of this variability in consumption, it is difficult to determine whether the char were overwhelmed by smolt abundance or satiated. This observed variability in consumption may be due to individual char migrating from the local lake area to the river at different times, thereby causing variable feeding durations.

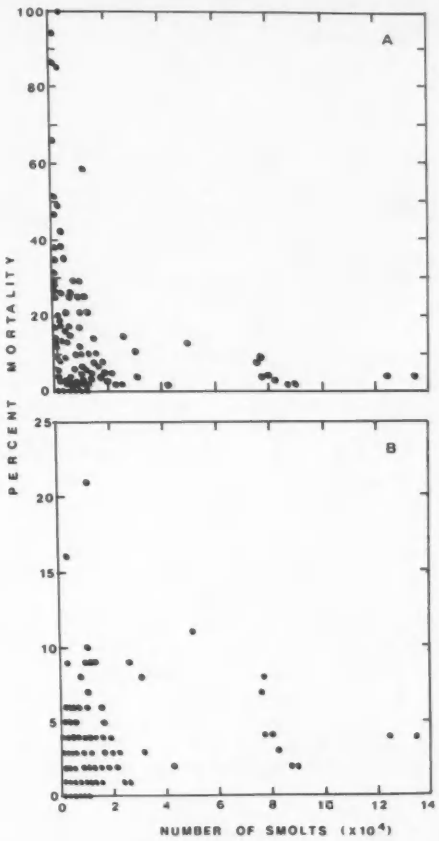

FIGURE 6.—Percent mortality at various levels of smolt abundance. (A) Entire population of 1,100 Arctic char fed each day; (B) number of feeding char equaled $1{,}100\,(1 - e^{-0.00004M})$, where M = number of migrating smolts.

distribution of smolts in the migration indicates the vulnerability of the smallest and largest smolts (Fig. 7). The large peaks represent age I smolts and the smaller peaks to the right are age II smolts. In each of the three time periods, the distribution of smolts from full char was consistently broader than the distribution of smolts in the migration, indicating that smolts average in length have a greater probability of escaping predation. The length distribution of smolts consumed by less full char was also broader than the distribution of smolts in the migration, but was skewed to the right. Thus, a greater proportion of age II smolts was consumed by less full char and to a lesser extent by full char than proportionately available in the migration.

When smolts consumed by full and less full char were combined, the average consumed smolt length was significantly larger than the average length from the migration ($\bar{d}$ = 0.1-1.1 mm, α = 0.05); however, the length distribution of the consumed smolts was similar to the smolt length distribution from the full char. This was due to the large proportion of smolts consumed by full char.

DISCUSSION

Char Functional Response

The functional response of char at Little Togiak River was similar to those reported for other salmon predators in one aspect (Ricker 1941; Cameron 1958; Hunter 1959; MacDonald *in* Foerster 1968). Because smolt abundance was usually low, char normally operated at the low end

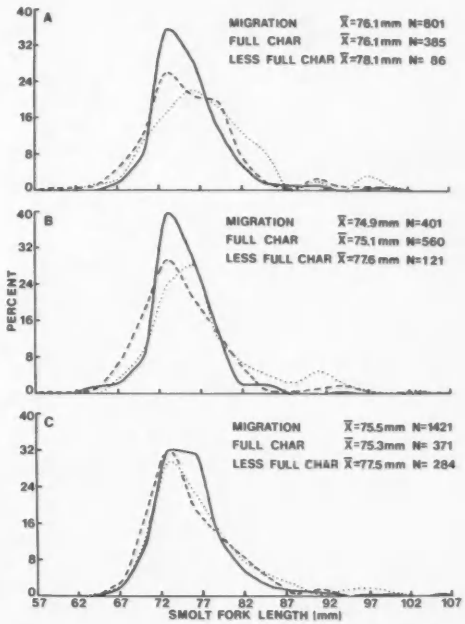

FIGURE 7.—Length distribution of smolts in the migration and in Arctic char stomachs according to stomach fullness. Solid line refers to smolts in the migration, dash line refers to smolts from full char, and dotted line refers to smolts from less full char. Sampling period from 9 to 15 June (A), 16 to 20 June (B), and 20 June to 17 July (C).

of their functional response where smolts could potentially be more vulnerable. Contrary to results of Ricker (1941) and Cameron (1958), consumption rates by char were proportional to smolt abundance and smolts did not find refuge at low migration numbers. On occasion (primarily in 1980) smolt abundance was great and consumption rates of char were disproportionately low, a response observed by Neave (1953). Thus, char at Little Togiak River exhibited a Type II functional response where vulnerability of smolts to predation may be greater at lower migration densities. This increased vulnerability ultimately depends on the numerical response of char to smolt abundance.

The inclusion of smolt weight and char length in the functional response multiple regression model further described important variables that influence char predation, as well as reducing within- and between-year variability. The exponential increase in consumption rates by char during migrations of smaller smolts is probably due to more smolts needed to decrease feeding activity and a greater ease in capturing small smolts. Because juvenile salmon growth is density dependent (i.e., smaller smolts at greater densities; Rogers 1968), increased consumption during migrations of smaller smolts may act to cancel the proportionately lower consumption rates of char at greater smolt abundances. Thus, it is important to test concurrently the effect of smolt weight and smolt density when describing the functional response of char.

The relationship of char length to consumption of smolts by char was best described by the allometric conversion (Moriarty 1977) of char length to char weight. According to regression analysis, the significance of char weight (as converted from char length) is questionable; however, char length was included in the model because it seems reasonable that a larger predator would require more food and may be able to capture mobile prey easier than a smaller predator. Rogers et al. (1972) reported larger char consumed more smolts than smaller char.

The average number of smolts consumed per char, as predicted by the model, was 0.8 smolts/24 h, and the maximum was 5.6 smolts/24 h. These values were corrected for smolt weight and char length. The low average of consumed smolts reflects the low number of smolts that generally migrate. The predicted maximum of 5.6 smolts/char corresponds quite well with the observed maximum of 6.0 smolts/char per 24 h. These estimates are lower than the average and maximum consumption rates by char at the Agulowak River (3.4, 8.4 smolts/char per 24 h, respectively) calculated from weekly estimates (Meacham and Clark 1979). This difference between the two rivers may be explained, in part, by the larger char size (Moriarty 1977) and the probable extension of the daily migration period at the Agulowak River, which is a large river that intercepts smolts from several lakes in the Wood River system.

Percent Smolt Mortality

The shape of a percent-mortality curve can provide valuable information on the stability characteristics of a salmon population (Peterman 1977) and provide information to a hatchery manager planning to release smolts. For example, percent smolt mortality could vary as in a Type III or modified Type II curve where smolt mortality increases up to a certain threshold density of smolts before decreasing. In this example, a hatchery manager should release smolts at densities greater than the threshold density.

Results from this investigation indicate the char numerical response (number feeding) may influence the type of percent-mortality curve. If the char numerical response is constant, then percent mortality will decrease as more smolts migrate. However, if the numerical response of char varies with smolt abundance, as we suspect, then percent mortality may increase with more smolts up to a threshold density. Beyond this threshold density, percent mortality decreases. The importance of the percent-mortality curve is to indicate the smolt density at which mortality is minimized. Smolts at Little Togiak River experience less risk of predation at daily migration abundances of about 20,000 smolts or greater. However, migration densities of this magnitude were rare.

Char Consumption of Smolts by Length

Char with less full stomachs contained smolts that were, on average, significantly larger than those in full char and those in the migration. A plausible explanation for the greater average smolt length in less full char than full char involves the effect of hunger on feeding behavior. Char containing only a few smolts may be hungry and aggressive (Ware 1972), which may induce a high success rate when feeding on the larger, more mobile smolts. When char approached stomach fullness, their hunger and aggressiveness may

have been lower, thereby reducing their success rate when attacking the larger smolts in the migration.

The larger smolts in less full char as compared with average smolt length in the migration may be due to the relationship between light intensity, migrating smolt size, and decreased feeding activity by char during the darkest portion of the night. Smolts migrating at night were significantly shorter than those migrating during the day (Ruggerone 1981; Burgner 1962; Aspinwall 1963). Feeding activity of char was observed to decrease substantially during the darkest 1-2 h of the night (often char would leap from the water while feeding). Also, hook and line fishing with lures was notably less effective during darkness. Therefore, the difference in average length of smolts consumed by less full char and those in the migration resulted from a decrease in smolt consumption when smolts in the migration were smaller. These results indicate that predation may be reduced by releasing hatchery salmon during the night.

The difference between smolt length in all char and length in the migration was relatively small. In part, this was due to the large proportion of smolts observed in full char, which was related to high smolt abundance. Because fewer char will reach stomach fullness during years of fewer smolts, the difference between length of smolts consumed and length in the migration is likely to be greater.

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FEEDING ECOLOGY OF WALLEYE, *STIZOSTEDION VITREUM VITREUM*, IN THE MID-COLUMBIA RIVER, WITH EMPHASIS ON THE INTERACTIONS BETWEEN WALLEYE AND JUVENILE ANADROMOUS FISHES[1]

The walleye, *Stizostedion vitreum vitreum*, is widely distributed in the United States and Canada and has been studied throughout most of its native range (Colby et al. 1979). The walleye is exotic to the Pacific Northwest and its biology here has not been fully investigated. The exact circumstances of walleye introduction into the Columbia River system are not documented; however, this piscivorous, cool-water fish is found throughout the mid-Columbia River (Fig. 1) and downstream of Bonneville Dam (Durbin[2]). As populations of walleye in the Columbia River have increased and their range extended, interest in them has focused on the potential sport fishery for walleye and on the impact of walleye on native salmonid populations (Carlander et al. 1978; Brege 1981).

[1]Technical Paper No. 6722, Oregon Agricultural Experiment Station, Oregon State University, Corvallis, Oreg.

[2]Durbin, K. 1977. News column. Oregon Department of Fish and Wildlife, Portland, Oreg.

FIGURE 1.—Map of the lower and mid-Columbia River showing the locations of the major dams and the John Day pool study area where walleye were collected during 1980 and 1981.

Construction of dams has transformed the Columbia River into a series of low velocity impoundments with physical characteristics (Table 1) that are well suited for walleye (Colby et al. 1979). Thus, the Columbia River fits the model for ideal walleye habitat proposed by Kitchell et al. (1977). This transformation has increased the time required for emigration of juvenile salmonids and increased their mortality partly due to increased predation (Raymond 1979).

The purpose of this study was to describe the spring and summer feeding ecology of walleye in the John Day pool of the Columbia River. Emphasis was placed on walleye interaction with juvenile salmonids and young-of-the-year American shad, *Alosa sapidissima*, an anadromous fish that is morphologically and behaviorally similar to outmigrant salmonids and is abundant in the Columbia River in the late summer. We concentrated on seasonal variation in walleye diets, diel feeding periodicity, and food selection as influenced by walleye size. Preliminary findings regarding the spring diets of these walleye were reported by Maule (1982).

TABLE 1.—Summary of limnological data for the John Day pool of the Columbia River, from Hjort et al. (1981). All data collected in August 1979, except for surface temperatures, which were taken in 1981.

Characteristic	Range for John Day pool	Range for study area
Water velocity (m/s)	0.1 - 1.4	0.5 - 1.4
Secchi depth (m)	1.0 - 2.2	1.5 - 1.7
Dissolved O_2 (ppm) surface-bottom	16.0 - 8.0	14.0 - 10.0
Average surface temperature Apr.-July-Sept. (maximum)	7.0°-24.5°-20.5(24.8°)°C	
Temperature profile surface-bottom	22.0° - 20.8°C	21.0° - 21.0°C
Pool width (km)	0.8 - 4.2	0.8 - 1.8
Midpool depth (m)	11 - 48	11 - 20
Pool length (km)	≈120	23

Methods

We collected walleye for this study in the first 23 km of the John Day pool immediately downstream from McNary Dam on the Columbia River (Fig. 1) from 2 April to 30 September 1980 and from 30 March to 30 September 1981. During each month we attempted to collect a minimum of 10 walleye during each of four generalized times of day: dawn, midday, dusk, and night. In 1980 we captured

walleye with either a 38.1 × 1.8 m sinking gill net with multifilament, variable, stretched mesh of 3.81, 5.08, 6.35, 7.52, and 10.16 cm, or a 76.2 × 3.7 m monofilament, floating gill net with 15.25 cm stretched mesh. All gill net sets were set at a maximum of 2.5-h duration in order to minimize regurgitation or digestion of stomach contents of the walleye. In 1981 we used gill nets and a 6.15 m electroshock boat with a 3,500-W generator and front mounted electrodes utilizing pulsed direct current at 1-4 A. Potential prey fish were periodically sampled with a 30.48 × 2.44 m beach seine of 6.35 mm stretched mesh. When we caught potential prey by means of gill nets, seines, or electroshock gear, we recorded numbers and fork lengths by species. Gear selectivity prohibited reliable estimates of numerical abundance of species, however, we used catch per unit of effort (CPUE) to estimate change in intraspecific abundance through time.

For each walleye captured, we recorded fork length (FL, mm), weight (g), sex, and stage of maturity, took scale samples, and preserved the stomach in 10% buffered Formalin[3]. Subsequently, each stomach was examined and each prey item was identified to the lowest possible taxon and its volume was recorded. A reference bone collection of potential prey species aided in the identification of partially digested prey. The most useful bones were pharyngeal teeth, opercles, preopercles, and jaw bones. Characteristics of the internal morphology, e.g., the black peritonium of bridgelip suckers, *Catostomus columbianus*, or the number of pyloric ceca in salmonids (Scott and Crossman 1973), were also useful in identifying prey items.

We separated stomach content data into subpopulations based on season and year of capture, and tested for statistically significant differences in numbers and volumes of individual prey items. We computed statistical significance using a nonparametric, multivariate test, $L_{N,t}$, which has approximately a chi-squared distribution with $p(v-1)$ degrees of freedom, where p is the number of conditions (prey taxa) and v is the number of populations (Koch 1969). To identify changes in the importance of food items we examined changes in the Index of Relative Importance (IRI), which is equal to the sum of the percent by volume and the percent by number, multiplied by the percent frequency of occurrence (Pinkas et al. 1971).

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Seasonal Diet

The walleye size ranges were similar for both years, about 200-750 mm FL (Fig. 2). In both years fish accounted for over 99% of the total prey volume (Tables 2, 3). Based on IRI (Table 4), prickly sculpin, *Cottus asper*, was the most important species found in walleye stomachs. Excluding un-

TABLE 2.—Percent by volume, percent by number, and percent frequency of occurrence of foods found in the stomachs of walleye collected in the John Day pool of the Columbia River April-September 1980. Sample size equals 189 walleye, with 38.1% empty stomachs. (Raw data are in parentheses.)

Prey taxon	% volume (ml)[1]	% number[1]	% occurrence
Salmonidae (juvenile)	5.5 (89)	8.7 (22)	12.8 (15)
Oncorhynchus tshawytscha	1.7 (27)	2.7 (7)	8.5 (10)
Unidentifiable Salmonidae	3.8 (62)	6.0 (15)	4.3 (5)
Castostomidae	39.4 (638)	6.0 (15)	12.0 (14)
Catostomus columbianus	7.3 (118)	2.0 (5)	4.3 (5)
C. macrocheilus	12.8 (200)	1.2 (3)	2.6 (3)
Unidentifiable Catostomidae	19.3 (320)	2.8 (7)	5.1 (6)
Cyprinidae	15.2 (247)	5.6 (14)	12.0 (14)
Acrocheilus alutaceus	2.2 (36)	3.2 (8)	6.8 (8)
Mylocheilus caurinus	11.8 (192)	1.2 (3)	2.6 (3)
Ptychocheilus oregonensis	0.4 (6)	0.4 (1)	0.9 (1)
Unidentifiable Cyprinidae	0.8 (13)	0.8 (2)	1.7 (2)
Miscellaneous fishes	40.0 (646)	75.4 (190)	85.6 (101)
Cottus asper	33.7 (544)	30.6 (77)	32.5 (38)
Lampetra spp.	0.1 (2)	0.4 (1)	0.1 (1)
Alosa sapidissma (juvenile)	1.9 (30)	9.9 (25)	7.7 (9)
Unidentifiable	4.3 (70)	34.5 (87)	45.3 (53)
Invertebrates	0.04 (0.7)	4.4 (11)	7.7 (9)
Ephemeridae	0.03 (0.56)	2.4 (6)	5.1 (6)
Chironomidae	<0.01 (0.04)	1.2 (3)	0.9 (1)
Talitridae	<0.01 (0.05)	0.4 (1)	0.9 (1)
Gammaridae	<0.01 (0.05)	0.4 (1)	0.9 (1)

[1]Volumes and numbers of individual prey taxa were significantly different from those of 1981 ($P < 0.005$).

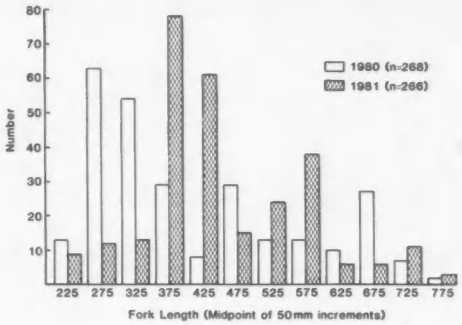

FIGURE 2.—Length-frequency distribution of walleye collected from the John Day pool of the Columbia River, April through September 1980 and 1981.

identifiable fish remains, the next most important foods were catostomids (largescale suckers, *Catostomus macrocheilus*, and bridgelip suckers) and cyprinids (primarily chiselmouth, *Acrocheilus alutaceus*, and peamouth, *Mylocheilus caurinus*). These species are generally associated with the benthos (Scott and Crossman 1973; Wydoski and Whitney 1979). In 1980, juvenile salmonids, primarily chinook salmon, *Oncorhynchus tshawytscha*, and juvenile American shad were equal to cyprinids in importance; however, in 1981, the importance of salmonids and shad was greatly reduced (Table 4).

All statistical tests were conducted with foods at the lowest taxon, and the data for individual species are presented in Tables 2, 3, and 4; however, in the interest of concise reporting we discuss results based on the following groups: catostomids, cyprinids, salmonids, cottids, shad, and invertebrates. Numbers and volumes of individual prey were significantly different between 1980 and 1981 ($P < 0.005$); to further investigate these differences, we tested for seasonal variation within and between years. We found no significant difference in numbers or volumes of prey between spring (April-June) 1980 and spring 1981 ($P > 0.25$); however, there were significant differences in diets (numbers and volumes) between summer (July-September) 1980 and summer 1981 ($P < 0.05$) and between the spring and summer of each year ($P < 0.01$).

We examined seasonal changes in IRI to detect which prey could account for significant differences in walleye diet (Table 4). From 1980 to 1981 there is a reduction in the importance of salmonids, cottids, and shad, and an increase in importance of catostomids, cyprinids, and invertebrates. Seasonal changes are not consistent; however, there are reductions in importance of cottids, increases in importance of cyprinids, and no changes in importance of invertebrates from spring to summer each year. Our CPUE data (Table 5) reflect annual and seasonal changes in the abundance of juvenile shad, juvenile

TABLE 3.—Percent by volume, percent by number, and percent frequency of occurrence of foods found in the stomachs of walleye collected in the John Day pool of the Columbia River, April-September 1981. Sample size equals 236 walleye, with 39.0% empty stomachs. (Raw data are in parentheses.)

Prey taxon	% volume (ml)[1]	% number[1]	% occurrence
Salmonidae (juvenile)	3.6 (62)	4.4 (14)	7.0 (10)
Oncorhynchus tshawytscha	2.8 (48)	3.2 (10)	1.4 (2)
Unidentifiable Salmonidae	0.8 (14)	1.2 (4)	5.6 (8)
Castostomidae	32.5 (563)	11.4 (36)	18.1 (26)
Catostomus columbianus	11.6 (201)	2.5 (8)	4.2 (6)
C. macrocheilus	1.2 (21)	0.6 (2)	1.4 (2)
Unidentifiable Catostomidae	19.7 (321)	8.3 (26)	12.5 (18)
Cyprinidae	34.1 (590)	13.0 (41)	25.7 (37)
Acrocheilus alutaceus	28.3 (490)	5.7 (18)	11.1 (16)
Mylocheilus caurinus	1.8 (32)	2.5 (8)	5.6 (8)
Ptychocheilus oregonensis	1.7 (30)	1.6 (5)	2.8 (4)
Cyprinus carpio	0.3 (6)	0.3 (1)	0.7 (1)
Carassius auratus	0.5 (8)	0.6 (2)	1.4 (2)
Unidentifiable Cyprinidae	1.5 (24)	2.3 (7)	4.1 (6)
Miscellaneous fishes	29.3 (508)	58.2 (184)	77.8 (112)
Cottus asper	22.5 (390)	25.6 (81)	36.8 (53)
Alosa sapidissma (juvenile)	0.1 (1)	0.3 (1)	0.7 (1)
Ictaluridae	0.2 (4)	0.3 (1)	0.7 (1)
Unidentifiable	6.5 (113)	32.0 (101)	39.6 (57)
Invertebrates	0.5 (8.23)	13.0 (41)	11.1 (16)
Ephemeridae	0.3 (5.98)	12.0 (38)	10.4 (15)
Chironomidae	0.01 (0.20)	0.3 (1)	0.7 (1)
Gammaridae	<0.01 (0.05)	0.3 (1)	0.7 (1)
Astacidae	0.1 (2.00)	0.3 (1)	0.7 (1)

[1]Volumes and numbers of individual prey taxa were significantly different from those of 1980 ($P < 0.005$).

TABLE 4.—Index of Relative Importance (IRI) (Pinkas et al. 1971) of foods found in spring (April through June) and summer (July through September)

Prey taxon	1980 Combined[1]	Spring	Summer
Salmonidae	182 (1.7)	293 (2.5)	148 (1.2)
Oncorhynchus tshawytscha	37 (0.9)	99 (1.7)	104 (2.4)
Unidentifiable Salmonidae	42 (1.0)	51 (0.9)	4 (0.1)
Catostomidae	545 (5.0)	548 (4.6)	749 (6.1)
Catostomus columbianus	40 (0.9)	12 (0.2)	121 (2.7)
C. macrocheilus	36 (0.8)	12 (0.2)	66 (1.5)
Unidentifiable Catostomidae	113 (2.6)	226 (3.9)	37 (0.8)
Cyprinidae	250 (2.3)	98 (0.8)	491 (4.0)
Acrocheilus alutaceus	37 (0.8)	2 (<0.1)	162 (3.7)
Mylocheilus caurinus	34 (0.8)	62 (1.1)	16 (0.4)
Ptychocheilus oregonensis	1 (<0.1)		4 (0.1)
Other Cyprinidae	3 (0.1)		6 (0.1)
Miscellaneous fishes	9,879 (90.7)	10,859 (91.5)	10,795 (88.3)
Cottus asper	2,090 (48.6)	3,621 (62.8)	1,335 (30.7)
Alosa sapidissma	91 (2.1)		480 (11.1)
Other (unidentifiable fish; *Lampetra* spp., Ictaluridae)	1,784 (41.3)	1,677 (29.0)	2,012 (46.4)
Invertebrates	34 (0.3)	74 (0.6)	40 (0.3)

[1]IRI's are not additive across columns.

TABLE 5.—Catch-per-unit-effort (CPUE) for various juvenile (Juv.) and adult fishes caught in the John Day pool of the Columbia River, April-September 1980-81.

Seines

Dates	Effort Sets	CPUE Juv. chinook	Juv. shad	Juv. peamouth
Apr.-Jun. 1980	45	16.65	0	0
Apr.-Jun. 1981	37	10.70	0	0
Jul.-Sept. 1980	35	2.65	92.76	6.88
Jul.-Sept. 1981	39	1.36	42.87	5.77

Gill nets

Dates	Hours	Chiselmouth	Largescale sucker	Bridgelip sucker
Apr.-Jun. 1980	122	0.23	0.86	0.40
Apr.-Jun. 1981	212	0.32	0.90	0.67
Jul.-Sept. 1980	330	0.37	0.54	0.74
Jul.-Sep. 1981	154	0.31	0.84	0.61

peamouth, and juvenile chinook salmon. However, Sims et al. (1982) reported no significant seasonal differences in the estimated numbers of juvenile salmonids emigrating past the John Day Dam (53,000 and 44,000 daily from 21 April to 30 June and from 1 July to 28 September 1981, respectively), 90 km downstream of our study area. Similar estimates are not available for 1980, but the smolt emigration past the John Day Dam was estimated at 8.3 million (Sims et al. 1981) and 7.7 million (Sims et al. 1982) in 1980 and 1981, respectively. Unfortunately cottids, the most important food, were rare in our CPUE data for 1980, and in 1981, the electroshock CPUE was <0.1, a level too low to detect changes.

Seasonal shifts in walleye diets are often the result of high spring-time availability of aquatic insects and/or increased availability of prey fish in the summer (Eschmeyer 1950; Parsons 1971). In this study, invertebrates represented 4-13% of the numbers of prey items (Tables 2, 3), however they contributed little to the total caloric intake of the walleye because of their almost negligible volume and poor assimilation by walleye (Kelso 1972). Moreover, invertebrates did not exhibit significant seasonal variation in walleye dietary importance (Table 4).

Diel Periodicity

The mean index of fullness, measured as the volume of stomach contents (ml) divided by walleye body weight (kg), for all walleye sampled is plotted against time of capture (2-h intervals) in Figure 3. The shape of this curve suggests the

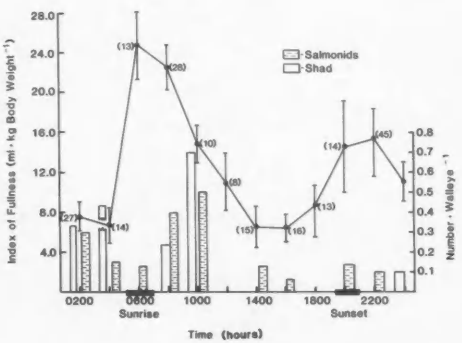

FIGURE 3.—Index of fullness and numbers of juvenile salmonids and shad consumed per walleye captured during 2-h intervals. Data collected from the John Day pool of the Columbia River, April to September 1980 and 1981. (Sample size in parentheses.)

stomachs of walleye collected in the John Day pool of the Columbia River in the 1980 and 1981. Numbers in parentheses are percent IRI.

Prey taxon	1981		
	Combined[1]	Spring	Summer
Salmonidae	56 (0.6)	53 (0.5)	58 (0.6)
Oncorhynchus tshawytscha	8 (0.2)	4 (0.1)	
Unidentifiable Salmonidae	11 (0.3)	26 (0.5)	58 (1.5)
Catostomidae	795 (8.8)	88 (0.9)	816 (8.3)
Catostomus columbianus	59 (1.4)	65 (1.1)	69 (1.7)
C. macrocheilus	3 (0.1)	1 (<0.1)	8 (0.2)
Unidentifiable Catostomidae	350 (8.4)	418 (7.3)	293 (7.3)
Cyprinidae	1,211 (13.4)	649 (6.3)	2,776 (28.4)
Acrocheilus alutaceus	377 (9.0)	462 (8.1)	298 (7.5)
Mylocheilus caurinus	24 (0.6)	1 (<0.1)	162 (4.1)
Ptychocheilus oregonensis	9 (0.2)	2 (<0.1)	41 (1.0)
Other Cyprinidae	34 (0.8)	1 (<0.1)	234 (5.9)
Miscellaneous fishes	6,808 (75.5)	9,480 (91.3)	6,028 (61.6)
Cottus asper	1,770 (42.2)	2,376 (41.7)	1,314 (32.9)
Alosa sapidissma	<1 (<0.1)		2 (<0.1)
Other (unidentifiable fish; *Lampetra* spp., Ictaluridae)	1,544 (36.8)	2,336 (41.0)	1,511 (37.9)
Invertebrates	150 (1.7)	113 (1.1)	106 (1.1)

same bimodal feeding periodicity as reported for other walleye populations during times of high prey densities (Swenson 1977). We found no annual or seasonal variation in this periodicity. Numbers of juvenile salmonids and shad consumed per walleye at various times of the day peak from late night to midmorning, drop to a low level at midday, and remain low through the evening peak in walleye feeding.

Size of Prey Consumed

Parsons (1971) showed a positive relationship between walleye length and length of prey consumed in Lake Erie. Walleye in the mid-Columbia River exhibit the same relationship, and size of prey is correlated to different prey taxa. The change in the percent of the IRI of various prey groups, as a function of walleye fork length, is

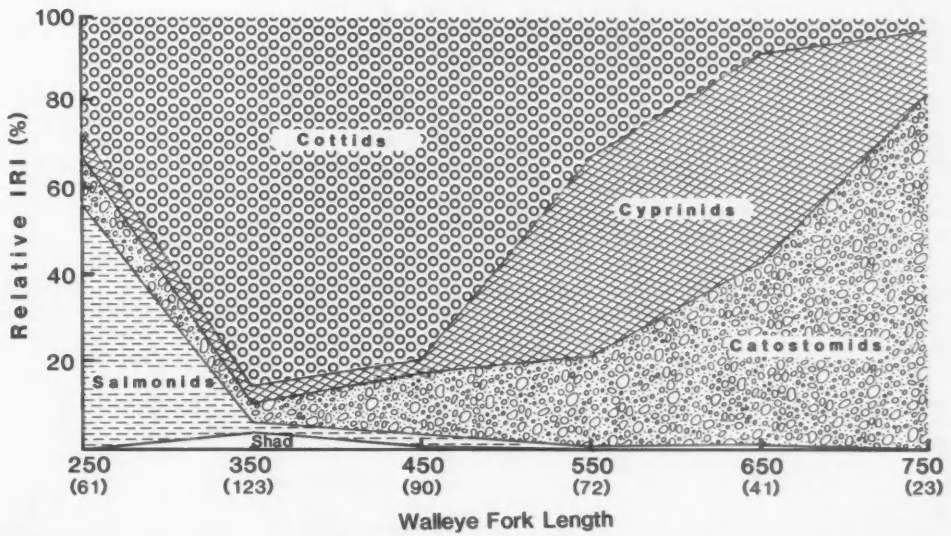

FIGURE 4.—Change in percent of total Index of Relative Importance (IRI) (Pinkas et al. 1971) of prey components as a function of walleye fork length (100 mm increments). Walleye collected in the John Day pool of the Columbia River, April through September 1980 and 1981. (Sample size in parentheses.)

charted in Figure 4. Small walleye (200-400 mm FL) primarily consume salmonids, cottids, and shad, while midrange walleye (400-600 mm FL) rely more heavily on cyprinids, cottids, and catostomids. For large walleye (>600 mm FL), suckers are the most important prey and the importance of cyprinids and cottids is reduced. Figure 5 contains the length frequencies of walleye prey collected in 1981 and shows peaks which correspond to the size of walleye most likely to consume that prey, i.e., cottids, juvenile shad, and juvenile salmonids are small (25-125 mm FL); cyprinids, excluding juvenile peamouth, are midrange in length (125-300 mm FL); and catostomids are present in a large range of sizes (150-450 mm FL) with peaks >300 mm FL.

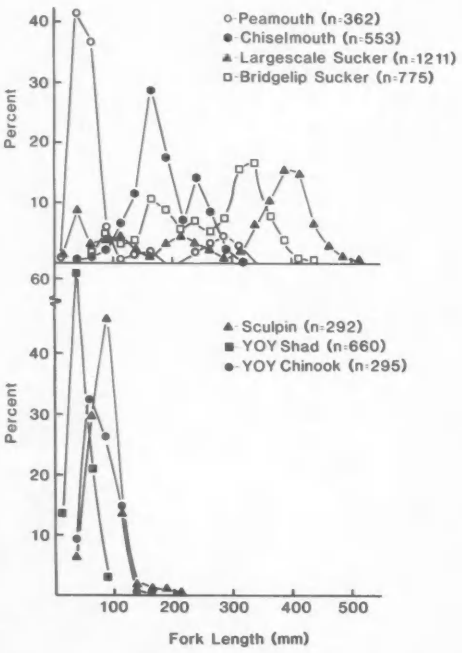

FIGURE 5.—Length frequencies of potential walleye prey collected in the John Day pool of the Columbia River, April through September 1981. (Sample size in parentheses.)

Discussion

Walleye have been described as opportunistic (Eschmeyer 1950; Ryder and Kerr 1978), crepuscular, or nocturnal feeders which primarily search the bottom for prey (Ali et al. 1977; Ryder 1977) and, in areas of abundant prey, select prey based on size preference (Parsons 1971; Wagner 1972). Walleye of the mid-Columbia River fit this general description; however, the species composition of their diet is different from that reported elsewhere. This difference is undoubtedly due to differing arrays and abundances of potential prey. Our data suggest no significant change in annual or seasonal variation in abundances of adult catostomids and cyprinids (chiselmouth) (Table 5); therefore, we believe that the variations in walleye diets (Tables 2, 3, 4) are the result of changes in availability of juvenile prey fish (Table 5).

Our data do not clearly explain the dietary role of juvenile anadromous fish that normally have seasonal abundances in excess of 10 million fish (Sims et al. 1981, 1982). We hypothesize that different behavioral responses of walleye, juvenile salmonids and shad, and alternate prey result in the walleye's apparent low dietary utilization of juvenile anadromous fish. The walleye's subretinal tapetum lucidum greatly enhances its visual acuity at twilight, when many potential prey have reduced visual acuity and are inactive (Ali et al. 1977; Ryder 1977). Yellow perch, *Perca flavescens*, are walleye's primary prey over most of their coextensive habitats (Colby et al. 1979), and the yellow perch's behavior in dim light is described as settling to the bottom and becoming inactive (Ryder 1977). Ali et al. (1977) suggested that were it not for their complimentary behavior at dawn and dusk, walleye and yellow perch interaction would not be as significant as it appears to be. In dimming light, emigrating juvenile Pacific salmon rise to the surface, increase swimming activity, and move downstream (Hoar 1958; Ali 1959). Similar behavior has been reported for juvenile shad (Loesch et al. 1982). Emery (1973) studied the diel movements of 21 species of Catostomidae, Clupeidae, Cottidae, Cyprinidae, and Percidae, and all but two species of Clupeidae were on or near the bottom at twilight and during the night. Emery (1973) further reported that these fish could be more closely approached by a diver at night than during the day. Therefore it appears that juvenile salmonids and shad are buffered from walleye predation by an abundance of alternate prey (Tables 2, 3, 5) of a wide size range (Figs. 4, 5) and by a separation in space and time during one of the walleye's peak feeding periods (Fig. 3).

We caught no walleye <200 mm FL (Fig. 2), even though our gear captured numerous specimens of other species <100 mm FL (Fig. 5). We

believe that inclusion of this smaller size group of walleye would not seriously alter our results or conclusions as they relate to predation on juvenile salmonids. They might, however, increase the importance of shad in walleye diets. Walleye <200 mm FL will primarily be juvenile walleye and will not reach 150 mm TL until mid-September (Brege 1981; Maule 1983). The length frequencies of juvenile chinook salmon which we sampled peaked at about 100 mm FL and, generally, chinook salmon complete their emigration by early fall (Raymond 1979; Sims et al. 1981). Juvenile shad, however, are generally smaller than juvenile salmonids (Fig. 5) and emigrate in late fall (Stainbrook 1983). Whereas juvenile salmonids may be buffered from the juvenile walleye predation by a size and time separation, juvenile shad may become a more important juvenile walleye food in late summer through fall.

This hypothesis is based on the current fish abundances within the John Day pool of the Columbia River. Should these abundances change, i.e., an increase in walleye abundance or a decrease in alternate prey, then we would expect a change in the walleye-juvenile anadromous fish interactions. The impact of walleye on the anadromous fish populations cannot be addressed without adequate estimates of walleye and prey fish abundances.

Acknowledgments

We thank Hiram Li and Carl Bond for their reviews of the manuscript. Funds were provided by the U.S. Army Corps of Engineers contract DACW57-79-C-0067, the Oregon Agricultural Experiment Station, and the Milne Computer Center, Oregon State University, Corvallis, Oreg.

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BATHYMETRIC DISTRIBUTION, SPAWNING PERIODICITY, SEX RATIOS, AND SIZE COMPOSITIONS OF THE MANTIS SHRIMP, *SQUILLA EMPUSA*, IN THE NORTHWESTERN GULF OF MEXICO[1]

The mantis shrimp, *Squilla empusa*, ranges in the western Atlantic Ocean from Maine through the Gulf of Mexico (Gulf) to Surinam (Manning 1969). This stomatopod occurs in high-salinity waters (Gunter 1950; Franks et al. 1972) and is one of the more common macrocrustaceans in the northern Gulf (Hildebrand 1954). *Squilla* sp. may be important predators of other crustaceans, polychaetes, and fish (Camp 1973; Caldwell and Dingle 1976), but they also serve as food for many fishes including *Rachycentron canadum*, *Lutjanus campechanus*, *Sciaenops ocellatus*, *Micropogonias undulatus*, and *Rhomboplites aurorubens* (Knapp 1951; Moseley 1966; Overstreet and Heard 1978a, b; Grimes 1979).

Despite its importance, little detail is known of the life history of *Squilla empusa*. The pelagic larval stages have been described (Morgan and Provenzano 1979; Morgan 1980), and much information has been published recently on the worldwide zoogeography and distributional interrelationships, evolutionary ecology, and life history patterns of stomatopods, primarily coral-dwelling taxa (Reaka 1979, 1980; Reaka and Manning 1980). However, the latter information does not deal with *S. empusa*, and it may not be valid to extrapolate to this species. Reaka (1979: table 5) reported that the coral-dwelling taxa were long-lived and gave estimates of 26-34 yr to reach median size (using mean growth increments and mean molting frequencies), 12-14 yr (using mean growth and maximum molting), or 4-8 yr (using maximum growth and molting). Although we could not determine age of *S. empusa* readily from length-frequency analysis, a much shorter maximum life span (1-3 yr) is part of what appears to be a common pattern of population dynamics in the white and/or brown shrimp communities where *S. empusa* occur (Chittenden and McEachran 1976; Chittenden 1977).

This paper describes bathymetric distribution, size at maturation, spawning periodicity, sex ratios, size compositions, and morphometric relationships for *S. empusa* collected in the northwestern Gulf during routine trawling operations.

[1]Technical article TA 18359 from the Texas Agricultural Experiment Station, Texas A&M University, College Station, TX 77843.

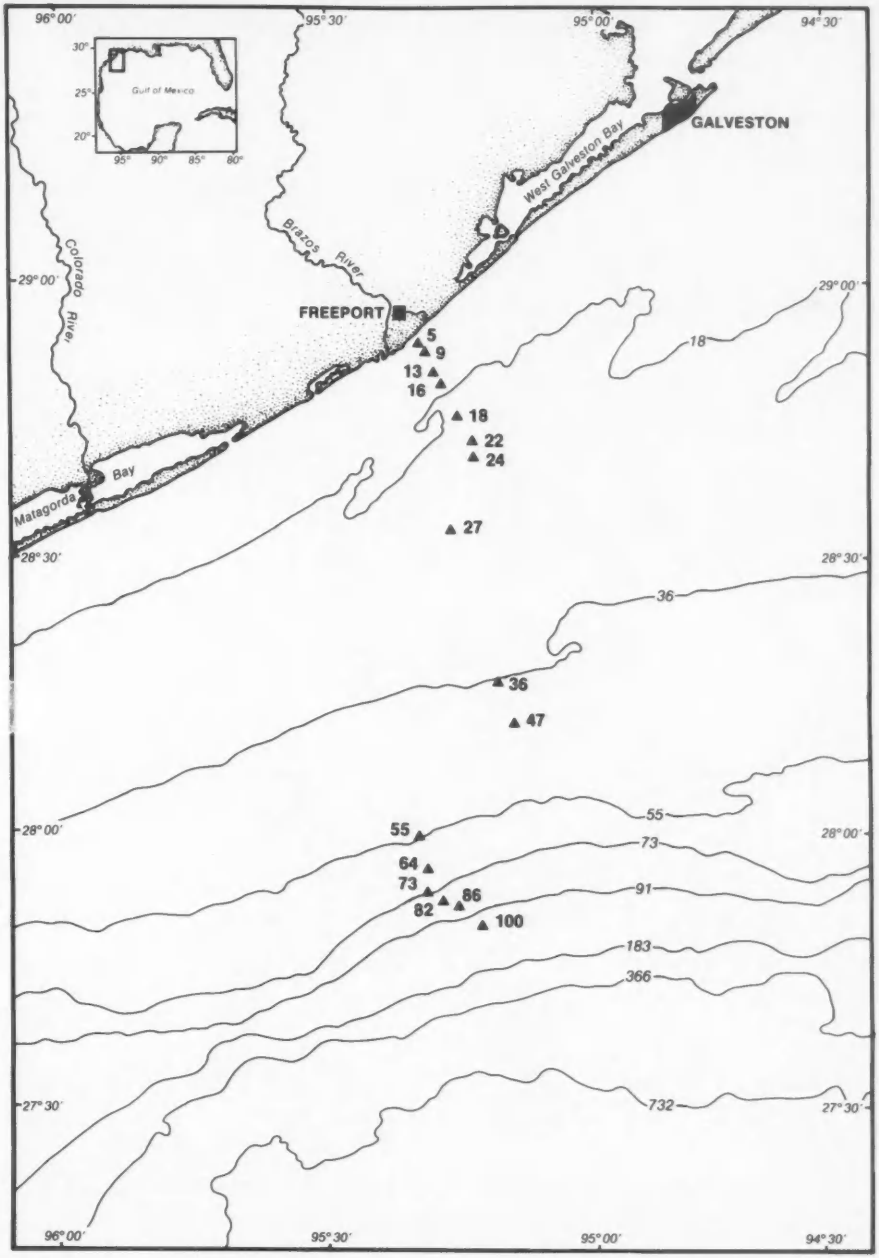

FIGURE 1.—Location of sampling areas. Station depths and bathymetric contours are indicated in meters.

Methods

Squilla empusa were collected fortnightly along a transect in the Gulf off Freeport, Tex. (Fig. 1) aboard a chartered shrimp trawler using twin 10.4 m (34-ft) trawls with a 4.4 cm stretched mesh cod end and tickler chain. Except for August and September 1979, a day and a night cruise were made each month in the period July 1979-October 1980 (Table 1). Data for *Squilla* were obtained from the first of two 10-min tows (bottom time) made at depths of 5, 9, 13, 18, 24, 27, 36, 47, 55, 64, 73, 82, 86, and 100 m, from 4 tows at 16 m, and from 12 tows at 22 m.

All *S. empusa* were culled from the catch, preserved in 10% Formalin[2], washed in fresh water, then stored in 70% ethanol. Specimens from the period July 1979-June 1980 were later processed to determine sex, total length (TL), and total wet weight (TW). Carapace length (CL), abdominal length (AL), abdominal width (AWD), and abdominal wet weight (AW) were measured on all specimens collected during seven cruises. Measurements follow Manning (1969), except that abdominal length was measured along the dorsal midline from the anteriormost portion of the first abdominal somite to the apices of the submedian teeth of the telson. Females collected during the period July 1979-October 1980 were assigned gonad maturity stages described in Table 2. Typical maximum size was approximated as a length l_L correlated with the Beverton-Holt yield model parameter t_L (Gulland 1969) following Alverson and Carney's (1975) definition that only 0.5-1% of the catch exceeds age t_L. All length measurements presented herein are total length unless stated otherwise.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Total length composition statistics (mm) by cruise for *Squilla empusa* from the Gulf of Mexico off Freeport, Tex., July 1979-October 1980. Night and day cruises are indicated by N and D.

Collection		n	Length (mm) Range	Mean	s	99% confidence limits of observations
5-9 July 79	N	695	26-132	85.7	17.1	41.7-129.7
19-22 July 79	D	6	77-108	88.2	14.0	31.8-144.6
22-25 Aug. 79	D	2	76-91	83.5	10.6	—
22-25 Sept. 79	D	491	37-124	71.7	14.3	34.9-108.5
2-6 Oct. 79	N	1,049	40-113	75.2	12.4	43.3-107.1
16-19 Oct. 79	D	458	47-109	75.0	11.1	46.4-103.6
3-6 Nov. 79	N	614	38-112	76.2	12.1	45.0-107.4
15-18 Nov. 79	D	72	51-96	71.0	9.5	46.5- 95.5
1-4 Dec. 79	N	137	53-102	75.4	11.9	44.7-106.1
14-19 Dec. 79	D	96	32-115	83.8	14.7	45.9-121.7
3-6 Jan. 80	N	857	29-123	77.0	15.5	37.1-116.9
16-20 Jan. 80	D	71	49-116	82.9	14.5	45.5-120.3
4-11 Feb. 80	N	948	33-116	78.6	15.1	39.7-117.5
15-20 Feb. 80	D	236	35-109	77.6	13.4	43.1-112.1
5-8 Mar. 80	N	680	34-113	79.2	11.8	48.8-109.6
19-23 Mar. 80	D	447	40-110	75.5	12.5	43.3-107.7
1-5 Apr. 80	N	197	37-106	77.1	12.7	44.4-109.8
16-20 Apr. 80	D	313	33-110	76.0	13.6	41.0-111.0
5-10 May 80	N	914	37-117	74.1	14.7	36.2-112.0
19-22 May 80	D	215	46-113	72.9	13.4	38.4-107.4
2-6 June 80	N	872	42-126	82.1	10.9	54.0-110.2
19-24 June 80	D	56	65-115	85.3	10.5	58.3-112.3
7-11 July 80	N	335	63-114	89.0	8.5	67.1-110.9
21-24 July 80	D	1	61	61.0	—	—
5-15 Aug. 80	N	478	32-122	75.5	15.6	35.3-115.7
26-29 Aug. 80	D	0	—	—	—	—
7-11 Sept. 80	N	74	54-115	84.2	11.9	53.5-114.9
22-25 Sept. 80	D	45	26-114	73.9	19.4	23.9-123.9
6-9 Oct. 80	N	60	46-117	83.2	12.3	51.5-114.9
20-31 Oct. 80	D	77	28-118	82.2	20.1	30.4-134.0

TABLE 2.—Descriptions of gonad maturity stages assigned to female *Squilla empusa*.

Stage	Description
1. Immature, Spent, or Resting	Ovaries narrow transparent tubes. We could not distinguish visually between immature, spent, or resting individuals, nor assign age based on length frequency analysis.
2. Early Developing	Ovaries with slight yellow coloration occupy 0-25% of abdominal cavity.
3. Late Developing	Ovaries with orange coloration occupy 25-50% of abdominal cavity; little or no expansion of ovaries within each segment.
4. Gravid	Ovaries deep orange in color occupy 50-100% of abdominal cavity; ovaries in each segment definitely expanded.

Results

Bathymetric Distribution and Diel Periodicity

Squilla empusa were collected from 5 to 86 m depths. Maximum abundance (male: 14.4-16.2 individuals/tow; female: 17.5-19.6 individuals/tow) occurred at 9-16 m (Fig. 2). Abundance was much lower at 5 m (male: 4.6 individuals/tow; female: 5.9 individuals/tow) and approximated that at 27 m. Abundance was even lower but uniform (<2.0 individuals/tow) from 36 to 55 m; only one specimen each was collected at 64 and 86 m.

Size compositions of *S. empusa* varied with depth, although trends were similar for each sex. Individuals from the entire observed size range (26-132 mm) occurred in depths of 5-27 m (Fig. 3); size compositions of each sex were similar throughout these waters. Deeper waters were occupied primarily by individuals in each sex greater than the average size of 77 mm. Few individuals <80 mm (<1%) occurred deeper than 27 m, and no individuals <80 mm occurred deeper than 55 m.

Catches of *S. empusa* were greatest at night. Mean catch/tow during the 1-yr period October 1979-September 1980, when both day and night

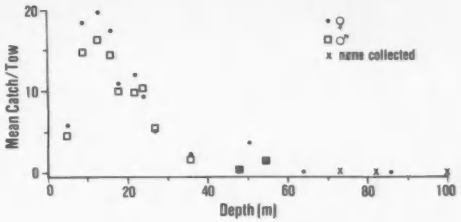

FIGURE 2.—Mean catch/tow (numbers) of *Squilla empusa* by depth for each sex.

cruises were made each month, was 6.79 during the day but 23.93 at night. The difference is significant at $\alpha = 0.01$ using a one-way analysis of variance ($F = 15.13$; 22 df), even though this simple model maximizes the error mean square in comparison to more complex models.

Size at Maturity and Spawning Periodicity

Squilla empusa begin to mature at 70 mm. No individuals <70 mm were in Early-Developing, Late-Developing, or Gravid stages (Fig. 4). Only a small fraction of all Gravid females (15%) were 70-80 mm, but half were gravid by 90 mm. There was little difference in size between individuals in the Early-Developing, Late-Developing, or Gravid stages, respective means being 88, 90, and 91 mm.

Spawning apparently occurs over an 8-mo period that begins in January and ends in July-August. Few or no Early-Developing, Late-Developing, or Gravid individuals were captured from September through December either year (Fig. 5). Individuals in these stages were abundant in January and remained so through July-August. Immature and Spent or Resting individuals greatly predominated during the period September-December each year.

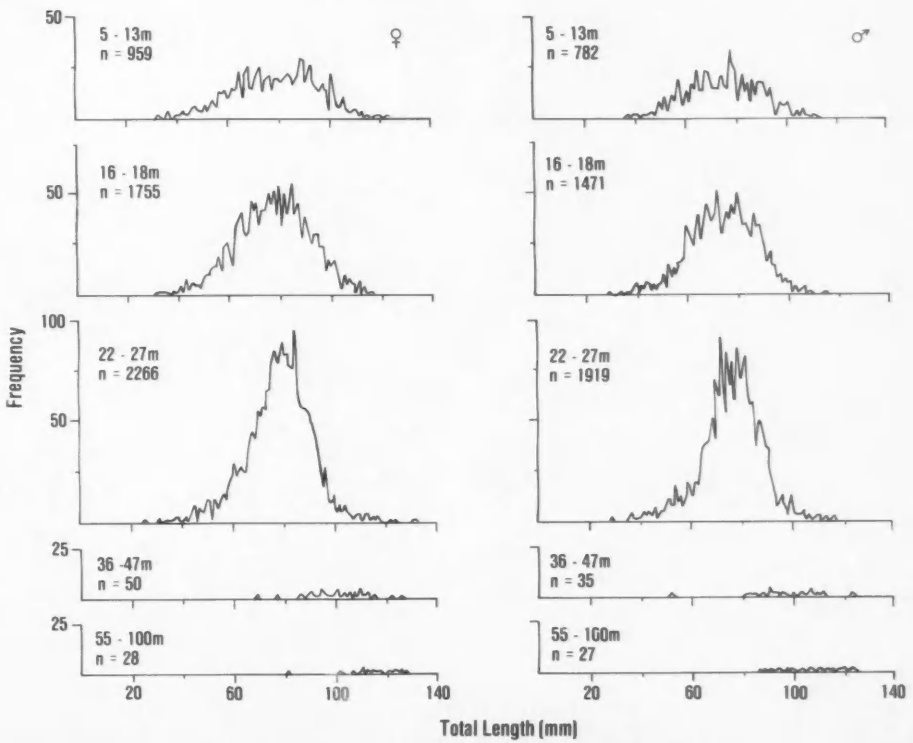

FIGURE 3.—Length frequencies of *Squilla empusa* by depth for each sex.

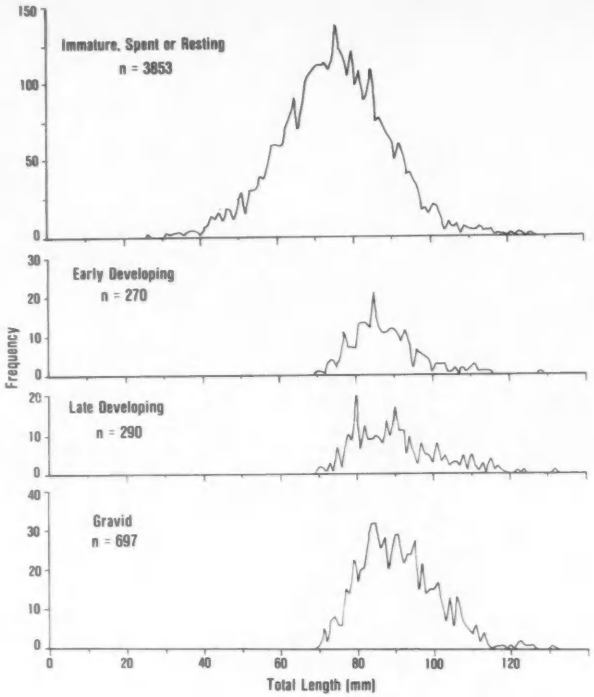

FIGURE 4.—Size of female *Squilla empusa* by maturity stage. Maturity stages are described in Table 2.

Sex Ratios

Females made up 54% of the overall catch of *S. empusa* and were significantly more abundant than males ($\chi^2 = 71.53$, $P < 0.05$). Except in August 1979 when only two individuals were caught, females predominated and made up 52-63% of the 500-1,000 *S. empusa* usually caught each month. Sex ratios did not differ significantly between depths ($\chi^2 = 1.82$, 4 df, $P > 0.05$). Sex ratios generally were equal from 30 to 80 mm, but females increasingly predominated at larger sizes (Fig. 6). Sex ratios did not differ significantly from a 1:1 ratio until *S. empusa* exceeded 80 mm (Table 3).

TABLE 3.—Observed sex ratios and chi-square statistics for *Squilla empusa* divided into 10 mm length groups, July 1979-June 1980. Asterisks indicate significant χ^2 at $\alpha = 0.05$.

Length range (mm)	No. individuals		χ^2
	Male	Female	
21-30	3	1	1.00
31-40	28	29	0.02
41-50	117	138	1.73
51-60	381	382	0.00
61-70	835	837	0.00
71-80	1,353	1,357	0.01
81-90	1,069	1,339	30.27*
91-100	387	699	89.64*
101-110	94	241	32.25*
111-120	19	69	28.41*
121-130	4	16	7.20*
131-140	—	2	2.00
Total	4,290	5,110	—

Maximum Size and Intrayear Variations in Size

Typical maximum size reached by *S. empusa* in the northwestern Gulf is 110-115 mm. The largest of 9,400 specimens we captured was only 132 mm, 99% were <110 mm, and 99.5% were <114 mm (Fig. 7).

Size compositions showed little change throughout the sampling period. Except for the

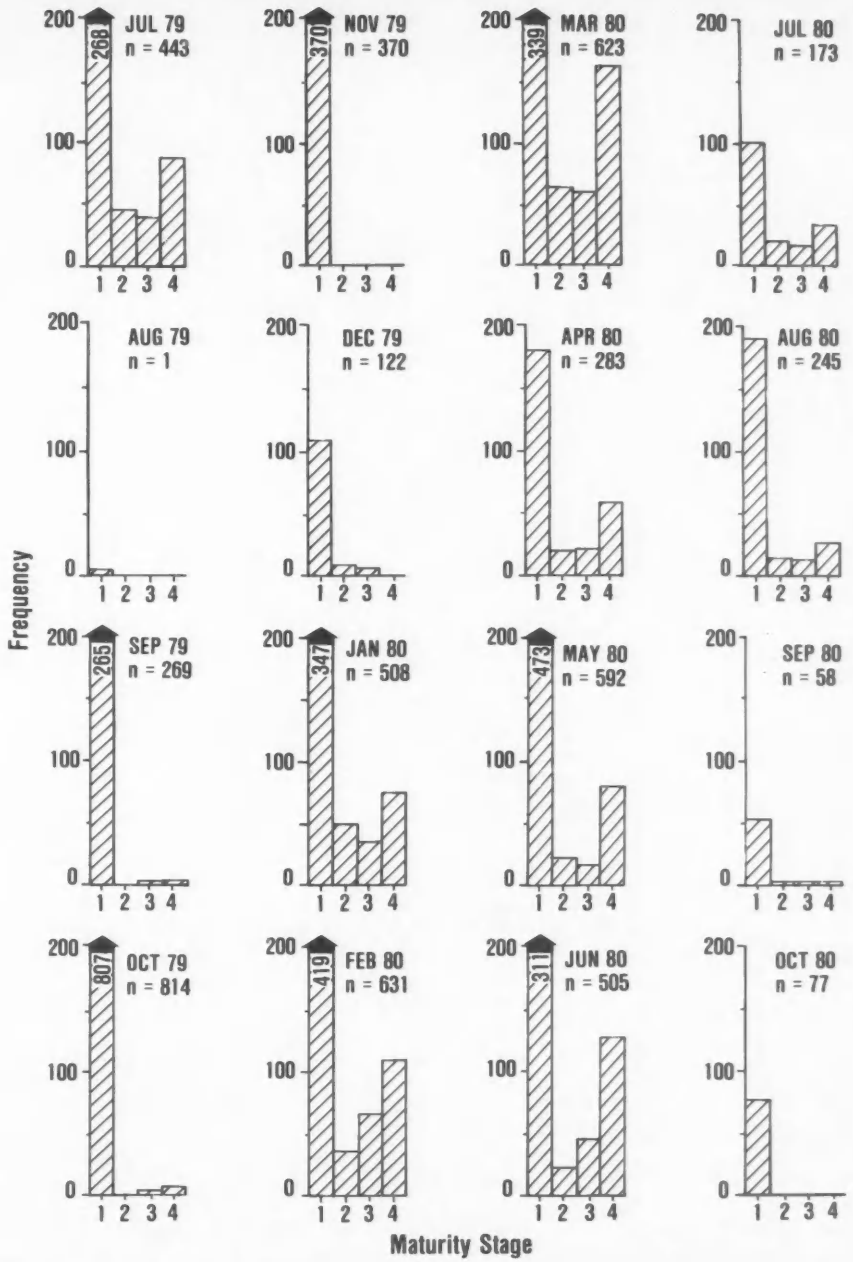

FIGURE 5.—Monthly numbers of female *Squilla empusa* by maturity stage for the period July 1973-October 1980. Stages (see Table 2) are 1) Immature, Spent or Resting, 2) Early Developing, 3) Late Developing, 4) Gravid.

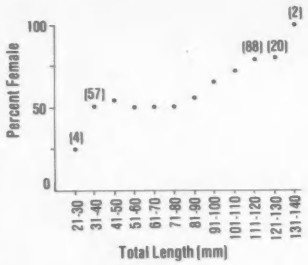

FIGURE 6.—Percentage of female *Squilla empusa* by size. Sample sizes are 255-2,710/size class, except where indicated.

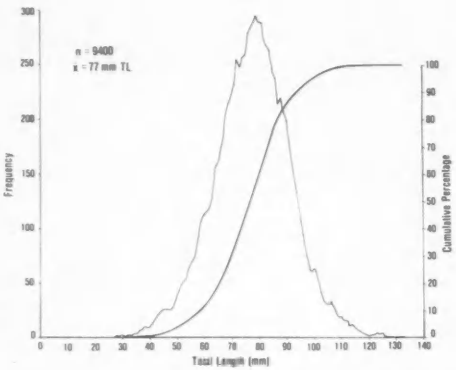

FIGURE 7.—Length frequency (moving averages of three) and cumulative percentage of all *Squilla empusa* collected off Freeport, Tex., July 1979-June 1980.

21-24 July 1980 day cruise when only one specimen was captured, mean sizes on each cruise ranged between only 71 and 89 mm (Table 1). In addition, 99% confidence limits for observations also showed little variation during this period.

Length-Weight-Width-Relationships

Length-length, length-weight, and length-width relationships are presented in Table 4. Length-weight regression coefficients were significantly different between the sexes ($F = 5.03$; 1, 9,381 df; $P < 0.05$). However, the minor difference ($b = 2.94$ vs. 2.96) may have little biological meaning, thus pooled regression statistics are also presented to simplify stock assessment. Calculated length-weight regression coefficients significantly exceeded $\beta = 3.0$ at $\alpha = 0.05$ (data pooled, $t = -12.23$; males, $t = -5.89$; females, $t = -10.42$).

Discussion

Bathymetric Distribution and Diel Periodicity

Squilla empusa occur on a mud or sandy-mud bottom (Franks et al. 1972) as do several of its congeners (Reaka and Manning 1980). This species ranges on such bottoms across most of the continental shelf in the northern Gulf. We captured *S. empusa* to depths of 86 m in agreement with Hildebrand (1954) and Franks et al. (1972), who captured specimens to 82 and 91 m, respectively. Our findings that *S. empusa* were common

TABLE 4.—Length-length, length-weight, and length-width regressions for *Squilla empusa*, sexes pooled unless indicated, with supporting statistics. Measurements are in grams and millimeters. Size range for each equation is 26-132 mm TL. All regressions are significant at $\alpha = 0.001$. Corrected total sum of squares is for y unless x is designated; r is from Ricker's (1973) GM functional regression. See below for definition of symbols.

Equation	n	$100\,r^2$ (%)	Residual Mean square	Corrected total sum of squares	r	$\bar{x}$
[1]CL = 0.82 + 0.20 TL	1,021	93.4	0.4345	6,728.42	0.21	76.74
TL = 1.21 + 4.70 CL	1,021	93.4	10.2521	158,764.13	4.86	16.09
AL = −0.36 + 0.62 TL	1,023	97.6	1.4486	62,048.05	0.63	76.70
TL = 2.40 + 1.58 AL	1,023	97.6	3.7213	159,395.26	1.60	46.92
AW = −0.01 + 0.63 TW	1,026	99.1	0.0423	4,963.75	0.63	7.13
TW = 0.08 + 1.58 AW	1,026	99.1	0.1067	12,505.14	1.59	4.46
AWD = −0.11 + 0.38 AL	1,028	94.6	0.5012	9,555.32	0.39	46.87
AL = 2.81 + 2.49 AWD	1,028	94.6	3.2828	62,590.81	2.56	17.70
AWD = −0.41 + 0.24 TL	1,023	93.9	0.5669	9,486.92	0.25	76.70
TL = 6.33 + 3.97 AWD	1,023	93.9	9.5249	159,395.26	4.10	17.72
All Data						
$\log_{10}$ TW = −4.7725 + 2.9430 $\log_{10}$ TL	9,383	97.7	0.0014	581.99; 65.65(x)	2.9774	1.88(TL) 0.76(TW)
Males						
$\log_{10}$ TW = −4.7974 + 2.9574 $\log_{10}$ TL	4,280	97.7	0.0014	247.66; 27.61(x)	2.9950	1.87(TL) 0.74(TW)
Females						
$\log_{10}$ TW = −4.7615 + 2.9362 $\log_{10}$ TL	5,103	97.8	0.0014	330.23; 37.47(x)	2.9686	1.89(TL) 0.78(TW)

[1]CL = Carapace length; TL = total length; AL = abdominal length; AW = abdominal wet weight; TW = total wet weight; AWD = abdominal width.

inshore of 24 m and most abundant at 9-16 m agree with Camp's (1973) data off west central Florida, but contrast with the data of Hildebrand (1954), who found greatest abundance at 35-42 m off Louisiana. *Squilla empusa* apparently reach peak abundance in much deeper water in the north central Gulf than off Texas, which may simply reflect the phenomenon that the inshore white shrimp community penetrates into deeper water there than it does in the northwestern area (Chittenden and McEachran 1976).

We captured greater numbers of *S. empusa* at night as did Hoese et al. (1968), who suggested that *S. empusa* retreat to burrows during the day and consequently are more likely to avoid trawls.

Spawning Periodicity

The prolonged spawning period of January to July-August that we found agrees, in part, with Franks et al. (1972), who collected stomatopod larvae in the plankton from April through September off Mississippi, and with Swingle (1971), whose limited data from Mobile Bay, Alabama, suggested winter and spring spawning. In addition, *S. empusa* 10-25 mm long occurred May-December in the stomachs of *Centropristis philadelphica* collected in conjunction with our study (Pavela and Ross[3]); *S. empusa* were most abundant in these stomachs in September and October. About 4-5 mo elapsed between our first collection of gravid *S. empusa* and their first appearance in *C. philadelphica* stomachs. These data suggest *S. empusa* spawn over an extended period of time and spend an extended time in the egg mass, propelagic, or pelagic stages of development, as occur in other closely related stomatopod species (Reaka 1979; Senta 1967 and Pyne 1972 cited in Morgan 1980).

Sex Ratios and Maximum Size

The change in sex ratio we observed at 80 mm, which is about the size at which females mature, may reflect different mortality rates between the sexes after maturity or growth cessation in larger males. Our data do not permit a choice between these possibilities.

The maximum size of 132 mm that we observed is similar to other maximum sizes for this species reported from the northern Gulf (Hoese et al. 1968, 120 mm SL; Christmas and Langley 1973, 145 mm). Much larger specimens have been reported from the Atlantic coast north of Cape Hatteras, N.C. (Bigelow 1941, 180 mm, type of length not given). These geographic differences in maximum sizes of *S. empusa* appear similar to differences in size that are found in many fishes (White and Chittenden 1977; Shlossman and Chittenden 1981; Geoghegan and Chittenden 1982; Murphy and Chittenden[4]). Therefore, our findings may reflect the zoogeographic change in population dynamics that these authors suggest occurs in the area of Cape Hatteras. Fishes, and possibly other taxa, as our data on *S. empusa* suggest, show smaller sizes, shorter life spans, higher mortality rates, younger age at maturity, more rapid turnover of biomass, and greater ability to avoid growth overfishing (see Gulland 1980) in the warm-temperate Carolinean Province waters of the Gulf of Mexico and South Atlantic Bight than do their conspecifics and congeners in the cold-temperate waters north of Cape Hatteras.

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DISTRIBUTION, LENGTH-WEIGHT RELATIONSHIP, AND LENGTH-FREQUENCY DATA OF SOUTHERN KINGFISH, *MENTICIRRHUS AMERICANUS*, IN MISSISSIPPI[1]

Populations of southern kingfish, *Menticirrhus americanus* (Linnaeus), are found in coastal waters from Long Island, N.Y., to Argentina (Stevens 1962; Miller 1965; Richards and Castagna 1970; Irwin 1970; Johnson 1978). Distribution appears to be continuous, but they are of greatest importance to commercial and sport fisheries along the South Atlantic and Gulf states. In 1978, 87,610 kg of southern kingfish valued at $36,085 were landed commercially in Mississippi (U.S. Department of Commerce 1977-78). Southern kingfish are caught incidentally by commercial fishermen using otter trawls in Mississippi coastal areas when fishing for shrimp or finfish such as croakers, red drum, and flounders. Southern kingfish ranked ninth in 1978 in economic value among commercial finfish species in Mississippi (third among trawl caught edible finfish) and is valued along the Gulf coast by sport fishermen who consider it an excellent food fish.

The majority of data available on southern kingfish is from studies conducted on the Atlantic coast (Welsh and Breder 1924; Hildebrand and Schroeder 1928; Irwin 1970). Little research has been conducted on southern kingfish in Mississippi, although information obtained on this species has been part of a large assessment program on finfishes along the Gulf coast (Christmas and Waller 1973; Loman 1978). Loman (1978) presented the only published works on length frequencies and length-weight relationships for southern kingfish in Mississippi.

The present study was conducted to investigate the distribution of southern kingfish in Mississippi coastal waters in relation to geographic range, season, temperature, and salinity. Length-weight relationship and length-frequency data are also presented.

Study Area

The study area consisted of the Mississippi coastal waters offshore to a depth of 91.4 m and included four estuarine systems: Biloxi Bay, Bay St. Louis, Pascagoula estuaries, and the smaller Pearl River system (Figs. 1, 2). Salinities and

[1]This paper is adapted from the author's unpublished Masters Thesis submitted to the University of Mississippi.

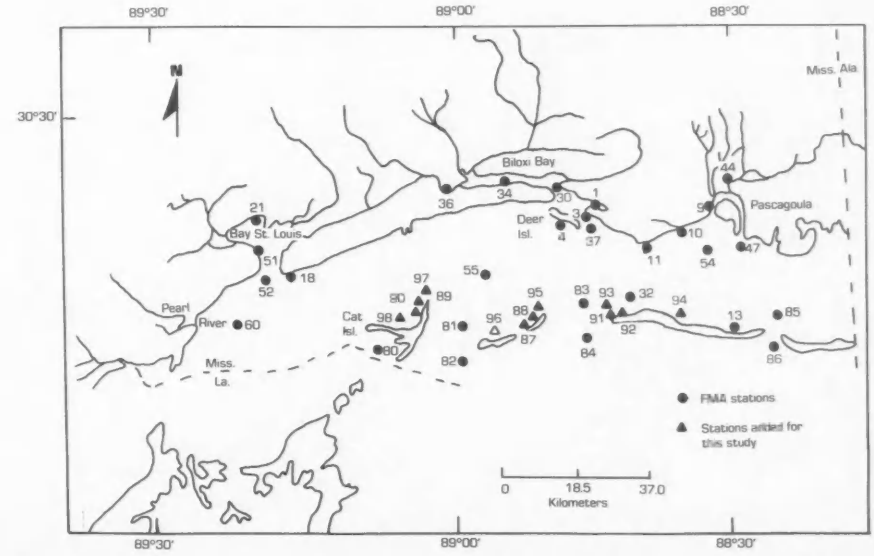

FIGURE 1.—Locations of stations for southern kingfish in estuaries, barrier islands, and offshore areas of the Mississippi Gulf coast sampled monthly.

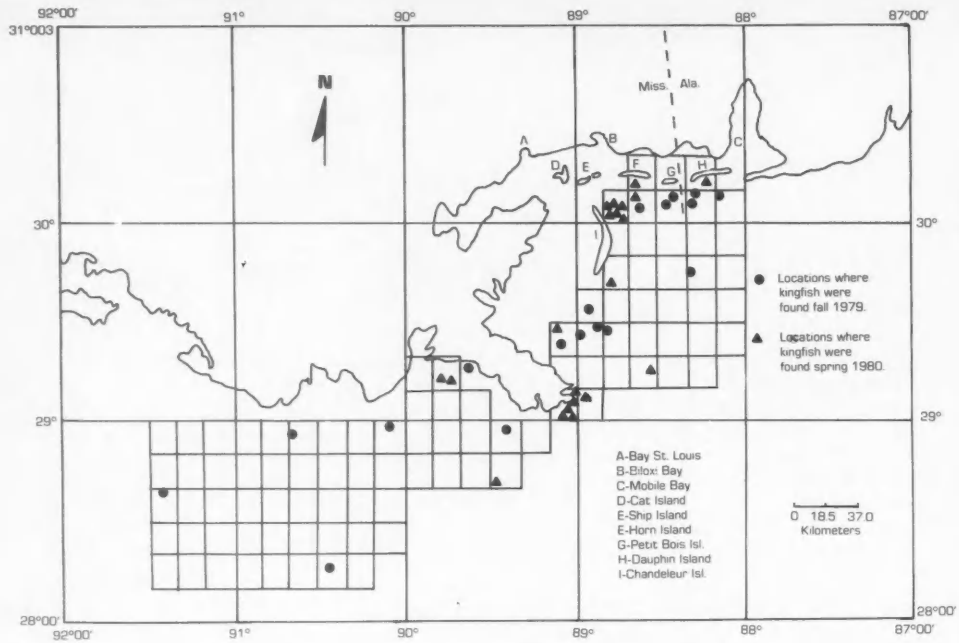

FIGURE 2.—Area of the Gulf of Mexico sampled for southern kingfish during the fall offshore cruise (25 October 1979 through 14 November 1979) and during the spring offshore cruise (10-18 April 1980). Grids represent station sites established by the National Marine Fisheries Service.

temperatures of the waters in these regions are influenced greatly by input from rivers and freshwater runoff. The estuaries drain into the Mississippi Sound which is bordered on the south by barrier islands. A complete description of the Mississippi Sound is given by Eleuterius (1978).

Areas sampled varied geomorphologically with location. Bottom types ranged from mud and silt in the rivers and upper estuaries to sandy tidal zones on the north side of the barrier islands. Overall depths varied from 0.3 m at seine stations to 91.4 m at offshore trawl stations. Sample areas in the estuaries ranged from 0.3 m to 12.2 m with relatively small tidal variations (0.1-0.6 m).

Materials and Methods

Monthly collections of southern kingfish were made from October 1979 through September 1980 (Fig. 1, Table 1), with the exception of stations 93 through 98 which were sampled monthly from February 1980 through September 1980. Twenty-eight of the stations were sampled in conjunction with the Fisheries Monitoring and Assessment Program at the Gulf Coast Research Laboratory, Ocean Springs, Miss. (Christmas 1978).

The type of gear used was dictated by the bottom topography and geographic location. At five stations along the barrier islands and in the estuaries, a 15.2 m bag seine with 6.4 mm bar mesh was used to collect juveniles. Larval and postlarval fish were collected by towing a Renfro beam plankton net (BPL) with 50 holes/cm² and a 1.8 m diameter mouth, in a 45.7 m semicircle at five stations. During the 10-min tows, young-of-the-year and adult southern kingfish were sampled with a 4.9 m standard otter trawl with 19.9 mm

TABLE 1.—Bottom salinities at monthly stations where southern kingfish were collected.

	Number of observations	Maximum salinity (‰)	Minimum salinity (‰)	Average salinity (‰)
Rivers	10	34.5	9.0	26.1
Estuaries	27	27.5	2.0	17.1
Mississippi Sound	37	33.0	14.5	24.7
Barrier Islands	29	29.0	5.0	22.2
Offshore	35	33.5	6.0	26.7

mesh, 6.4 mm tail mesh, and 0.9 m doors at 18 stations in the Mississippi Sound and with a 12.2 m standard otter trawl with 19.1 mm mesh, 6.4 mm tail mesh, and 1.3 m doors at 6 stations in the passes and outside the barrier islands. One sample was taken at each station per month, except at Fort Point (station 30) where two samples were taken: one with the 15.2 m seine and one with the BPL.

In the fall of 1979 and the spring of 1980, collections were made during National Marine Fisheries Service groundfish cruises (U.S. Department of Commerce 1979, 1980). Samples were taken by the RV *Oregon II* in depths of 9.1-91.4 m (5-50 fathom lines) from Mobile Bay, Ala., to Ship Shoal, La., extending to the east and west beyond Mississippi coastal waters (Fig. 2). Three successive 10-min tows were made at each station with a 12.2 m standard otter trawl with 19.1 mm mesh, a 1.22 m vertical opening, and 2.44 m doors, and samples were randomly taken. Specimens were frozen on board the ship, except ripe females which were preserved in 10% Formalin[2] for future use in fecundity estimates.

In the laboratory, each fish was weighed to the nearest 0.1 g and standard length measured to the nearest 1 mm. If the sample exceeded 50, a subsample of 50 was weighed and measured individually. The remainder of the catch exceeding 50 was counted and gross weight taken.

Salinity was determined with a refractometer (accuracy of 1‰) at stations sampled monthly, and on the groundfish cruises by titration at the National Marine Fisheries Service Laboratory (U.S. Department of Commerce 1979, 1980). Temperature was taken with a YSI Model 54 oxygen meter at monthly stations and with a centigrade thermometer on the groundfish cruises. Where a trawl was used, bottom water samples were collected with a Niskin or a Kemmerer bottle depending on the location and vessel used.

The length-weight relationship was calculated for southern kingfish by following the procedure of Rounsefell and Everhart (1953).

Results

Geographic Range

The distribution of southern kingfish in Mississippi extends from as far north as Bayou Bernard (station 36) to offshore beyond the barrier islands (Fig. 1). Fish were captured at all monthly sample sites at some time during the year except at seven stations where water depth ranged from 0.3 to 19.5 m.

During the fall groundfish cruise, southern kingfish were captured from 4.8 km south of the barrier islands to below the Mississippi River Delta and from long. 88°10′-91°25′W (Fig. 2). During the spring cruise the geographic range was about the same; however, populations were denser near the Chandeleur Islands and at the southern tip of the Mississippi River Delta. Catches of shrimp, a primary food of southern kingfish, were high in these areas, indicating the fish could have concentrated because of an abundant food supply.

Size of the southern kingfish captured varied with the geographic location. Specimens 50-150 mm SL frequented estuaries and inshore waters, while adults exceeding 150 mm SL were found on the Gulf of Mexico side of the barrier islands and offshore in waters as deep as 69.5 m. Distribution and size of the fish captured were also related to gear selectivity—trawls were used to capture adults in the passes and offshore, whereas smaller mesh gear types were more effective for obtaining juveniles and young-of-the-year in estuaries and inshore waters. Trawls accounted for 42% of the total catch at monthly sample sites.

Seasonal Distribution

A total of 1,554 southern kingfish was captured from October 1979 through September 1980. The numbers of fish gradually increased from December with a peak in February; from March through September there was no apparent numerical pattern (Fig. 3). On the other hand, the monthly catch by weight peaked in April with a lesser peak in January. Weight gradually declined during the remainder of the year.

Although overall catches for January and February were high, stations in the passes between the barrier islands and offshore accounted for the majority of southern kingfish in these months. Few southern kingfish were found in the estuaries during winter, and no kingfish were landed at any of the offshore stations during May, June, and July.

During the fall offshore groundfish cruise, 121 southern kingfish (100-280 mm SL) were captured. The spring cruise was more productive with 307 fish (70-270 mm SL) taken. No previous data on

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

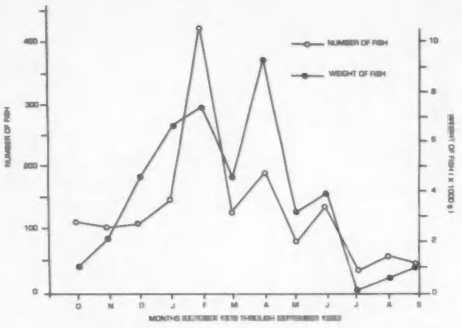

FIGURE 3.—Summary by number and by weight of the catch data for southern kingfish at stations sampled monthly from October 1979 through September 1980.

the distribution of this species in these offshore areas of Mississippi are available for comparison.

Salinity Range

Southern kingfish were captured in waters ranging in salinity from 2.0 to 36.6‰, with the majority found above 20.0‰ (Table 1). The mean salinity for the Mississippi coastal waters where southern kingfish occurred at regularly sampled stations was 23.4‰. During the fall groundfish cruise, bottom salinities where southern kingfish were taken ranged from 31.4‰ west of the Mississippi River Delta to 36.6‰ south of Horn Island, with an average bottom salinity of 34.5‰. No bottom salinities were available during the spring offshore cruise because of equipment problems.

Temperature Range

Young-of-the-year and adult southern kingfish were captured in waters with bottom temperatures ranging from 8.0°C in December to 37.3°C in August. The largest catches were taken in waters ranging from 20.0° to 30.0°C. Larval and postlarval fish (0.5-20.0 mm SL) were found from May through November in the shallow inshore waters and northern tidal zones of the barrier islands at temperatures ranging from 12.0° to 37.3°C.

The bottom water temperatures where southern kingfish were taken for the fall groundfish cruise ranged from 22.4° to 25.5°C (average of 23.2°C) and for the spring cruise ranged from 22.4° to 25.5°C (average of 22.3°C). In general, bottom temperatures on offshore cruises decreased with increasing depths.

Length-Weight Relationship

The length-weight relationship was calculated for the 1982 southern kingfish (ranging from 0.5 to 291.0 mm SL) by the following regression equation:

$$\text{Log } W = -4.48683 + 2.92908 \text{ Log } L$$

where W = weight in grams and L = standard length in millimeters (Fig. 4). The coefficient of determination R^2 was 0.9779.

Length-Frequency Data

At stations sampled monthly, southern kingfish juveniles (<50 mm SL) were most common from May through October; fish in the 100-150 mm SL range were fairly constant all year with a peak in March; and fish in the 150-250 mm SL range were rare during all months except April (Fig. 5). August was the only month where fish 10 mm SL or less were captured. The majority of the fish captured during the two offshore cruises were >100 mm SL with an average of 174 mm SL (Fig. 6).

The mean sizes of southern kingfish taken at the monthly stations were generally much smaller than those from the offshore groundfish cruises because young-of-the-year utilize the estuaries and inshore waters as nursery grounds. Gear selectivity must also be taken into account because the larger trawls used offshore are inefficient for capturing juveniles.

Discussion

Young-of-the-year frequented estuaries and inshore waters, while adult southern kingfish were found to be more abundant offshore in deeper waters. This was also reported by Pearson (1941) for the Chesapeake Bay area and by Geagan (1962) for the coastal waters of Louisiana. Irwin (1970) found the most common habitat for juveniles <50 mm SL to be open surf on sandy beaches, whereas in this study they occurred most often in sandy tidal zones of the barrier islands and estuaries.

High offshore catches and very low inshore catches from December through April support reports by Gunter (1938, 1945) and Christmas and Waller (1973) that adult southern kingfish migrate offshore during winter months and are summer residents of the estuaries. Similar reports were made by McIlwain (1978) for recreational

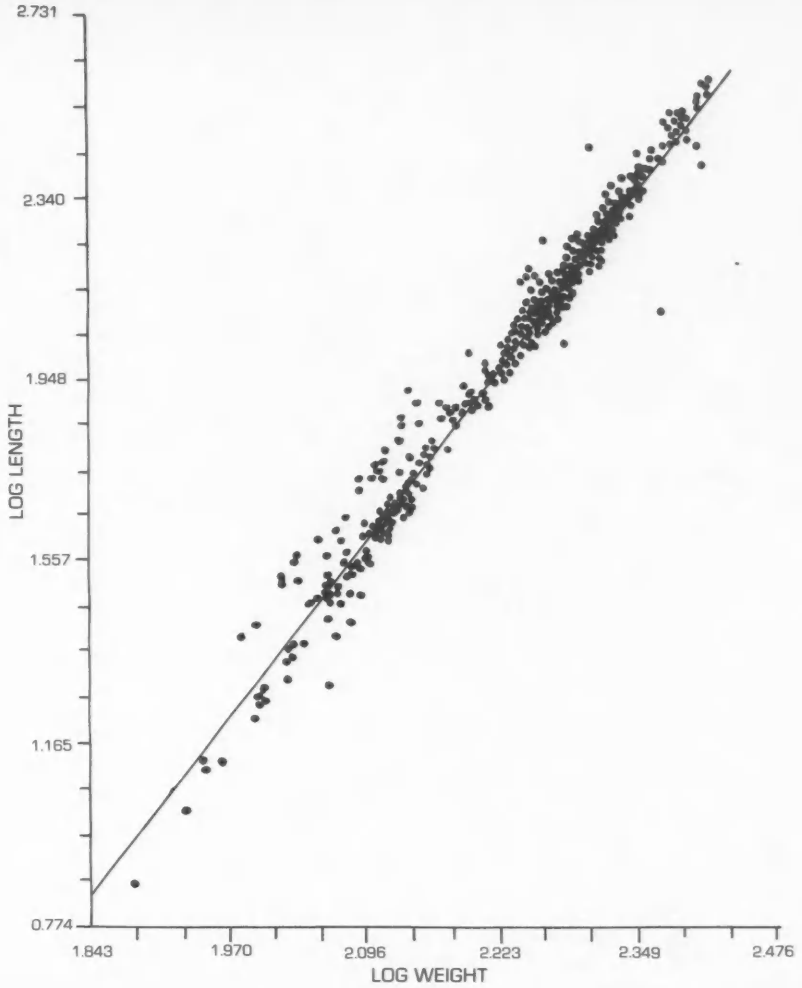

FIGURE 4.—Length-weight regression for all southern kingfish caught from October 1979 through September 1980.

catches from Biloxi Bay, Miss., and by Miller (1965) while trawling off Port Aransas, Tex.

The salinity range of 2.0-36.6‰ is slightly broader than the range of 5.0-35.5‰ reported by Christmas and Waller (1973). Loman (1978) reported that the highest catches of southern kingfish in Mississippi were between 15.0 and 30.0‰ and that mean length increased as salinity increased. The latter was also true in this study since larger fish were captured offshore where salinities were higher, and only postlarval and young-of-the-year fish were found in salinities below 15.0‰.

I concur with most authors that this species is eurythermal (Gunter 1945; Franks 1970; Christmas and Waller 1973; Loman 1978). While Loman (1978) reported southern kingfish in Mississippi coastal waters with temperatures as low as 7.0°C, the highest previously recorded temperature was 31.0°C reported by Springer and Woodburn (1960)

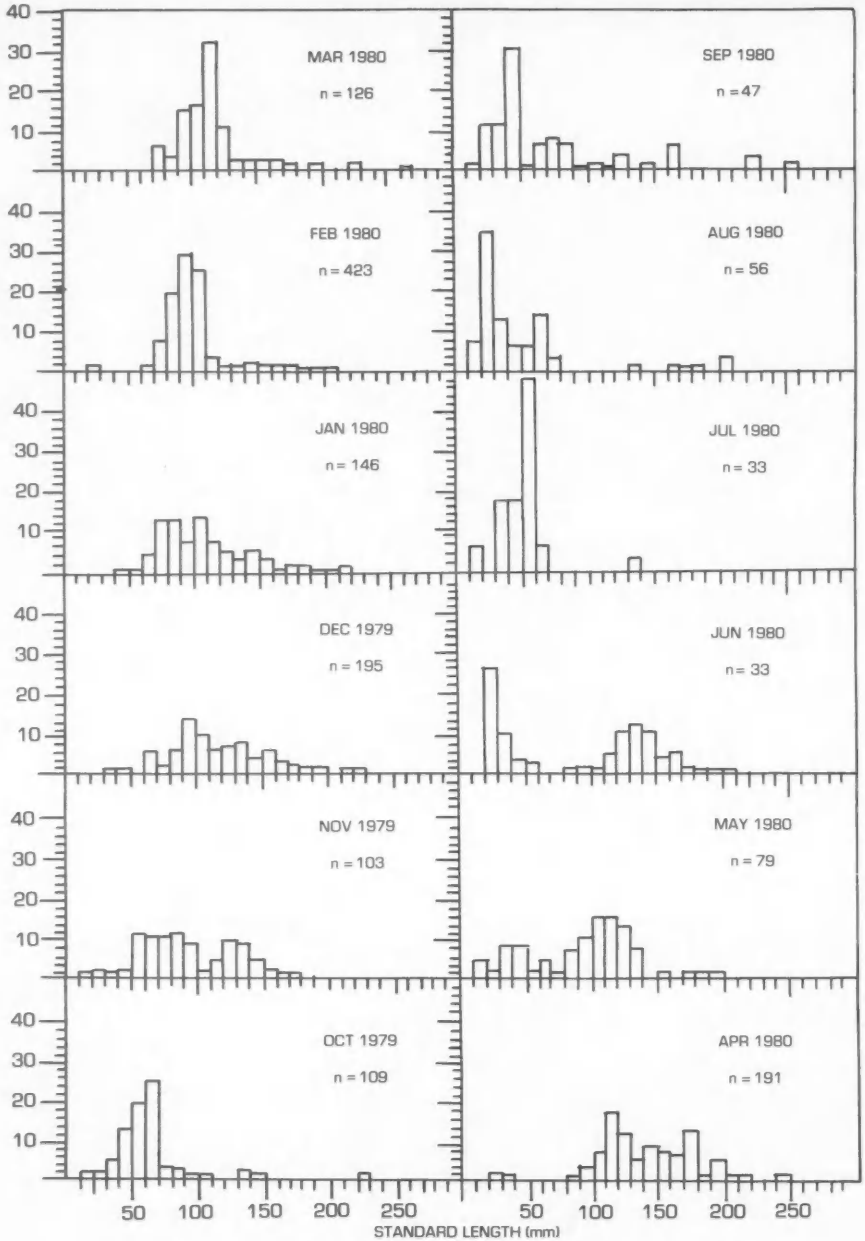

FIGURE 5.—Standard length frequencies of southern kingfish captured at regular monthly stations from October 1979 through September 1980. Total number of fish per month is represented by "n".

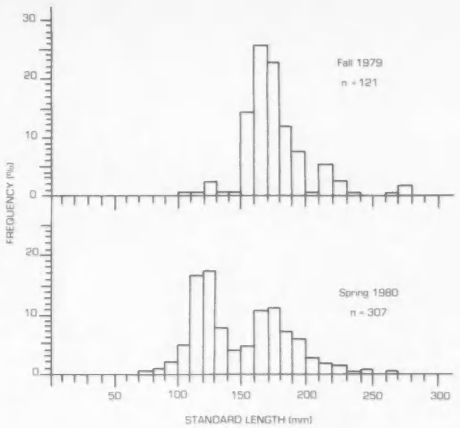

FIGURE 6.—Standard length frequencies of southern kingfish caught during the fall and spring offshore cruises in the Gulf of Mexico. Total number of fish per cruise is represented by "n".

in the Tampa Bay area. Loman (1978) reported a much narrower temperature range of 24.0-30.0°C for larval and postlarval fish (4.0-20.0 mm SL).

The length-frequency distribution recorded during 1979-80 is comparable to the published reports for 1973-76 (Loman 1978). Growth of southern kingfish is fairly consistent among individuals with the most rapid growth during the first year, as also reported by Hildebrand and Cable (1934) and Bearden (1963) for southern kingfish on the Atlantic coast. Young-of-the-year averaged about 100 mm SL by November. Bearden (1963) also reported southern kingfish in South Carolina to reach about 100 mm SL by November of the first year, whereas Hildebrand and Cable (1934) reported a slightly higher average of 135 mm TL by November of the first year in Beaufort, N.C.

Acknowledgments

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SCANNING ELECTRON MICROSCOPE EVIDENCE FOR YEARLY GROWTH ZONES IN GIANT BLUEFIN TUNA, *THUNNUS THYNNUS*, OTOLITHS FROM DAILY INCREMENTS

Atlantic bluefin tuna, *Thunnus thynnus*, are found throughout the Atlantic Ocean, the Mediterranean Sea, and the Gulf of Mexico (Gibbs and Collette 1967). Bluefin tuna are both commercially and recreationally important. Thus, it is important that the population dynamics of this species be understood in order that international policies can be developed.

Age determination and subsequent growth estimation are critical for tuna management. However, confusion and controversy surround age estimation in tunas. The earliest record of age and growth of tunas (probably bluefin) was by Greek fishermen nearly 2,000 yr ago as documented in Aristotle's "Historia Anumalium" (Bell 1964). In recent times, the aging of tunas has become much more important and has been critiqued by Hayashi (1958), Bell (1964), and Shomura (1966). These reviews point to the problems and difficulties in aging tuna. These problems and difficulties appear to be more evident in aging bluefin tuna.

Bluefin tuna are usually aged by counting growth increments on their hard parts. Vertebrae have provided acceptable ages (Rodríguez-Roda 1964; Butler 1971; Nichy and Berry 1976; Berry et al. 1976), but the aging of large or "giant" (>250 kg) bluefin tuna is suspect because the outer increments appear very close together. Otoliths have also been used to study age and growth of bluefin tuna (Butler et al. 1977). Berry et al. (1976) compared otolith age estimates with vertebra estimates and discovered a discrepancy. They found corresponding marks on both vertebrae and otoliths for the first 10 yr, but not thereafter, when otoliths had more incremental zones. They hypothesized that more than one incremental zone was deposited yearly in otoliths after the first 10 yr.

Daily increments in yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*, otoliths were studied by Wild and Foreman (1980) and Uchiyama and Struhsaker (1981). Taubert and Tranquilli (1982) used daily increments to verify annuli in the otoliths of large mouth bass, *Micropterus salmoides salmoides*, and it is proposed that an analogous investigation would provide corroborative evidence for the annual nature of outer major increments in giant bluefin tuna otoliths.

Methods and Materials

Sagittal otoliths were collected in November 1978, from giant bluefin tuna which were reared in the sea ranching program of St. Margaret's Bay, Nova Scotia, Canada. Fish were weighed and measured (TL) and the otoliths were collected as described by Caddy et al. (1976). All otoliths were washed in water and stored dry.

Whole otoliths from four fish were placed in epoxy resin and sectioned on a Buehler Isomet[1] saw. Sections 200 μm thick were acquired from the region judged to contain the core. A diagrammatic view of a cross section of a bluefin tuna otolith is

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

shown in Figure 1. Ten to 15 sections were sawed from each otolith. The number of sections viewed was dependent upon the clarity of the increments.

Each otolith section was fastened to an aluminum scanning electron microscope (SEM) stub with 5-min epoxy. The otolith section was highly polished with 0.3 μm alumina paste and etched with 6% EDTA (ethylenediaminetetraacetatic acid, adjusted to pH 8 with NaOH) for 1 to 20 min. The otolith sections were washed in water, dried, coated with gold, and viewed on a SEM at various magnifications. Observations and counts were made while the otolith section was in the SEM.

It was discovered that different areas of the rostral lobe of the otoliths were made clear by different etching times. Sequential etching made it possible to view microincrements in the outer 10 major increments. Individual sections were etched for different periods of time, with 15- to 20-min etching times showing the inner increments more clearly. The 10 outermost major increments were clearly visible in all sections and could be followed from section to section regardless of etching time. Each major increment was chosen to be from the center of one ridge to the center of the successive ridge; sequential etching revealed the microincrements between the ridges. It was not possible to count the microincrements from the edge of the otolith inward past the 10th major increment on any individual section. Consequently, sequential cross sections from each otolith were etched for different periods of time, in steps of 1 min, in order to follow the progression of the microincrements.

In the present study, a microincrement was defined as an unbroken incremental zone with discontinuous zones as boundaries (Radtke and Dean 1982) and was considered to be a daily increment.

Results and Discussion

SEM techniques made it possible to view microincrements in bluefin tuna otoliths from four individual fish. The most visually distinct increments were found on the rostral lobe of the otolith cross section (Fig. 1). Thus this area was used predominantly for SEM observations. The major increments of the otolith can readily be seen in Figure 2. Higher magnification (10,000 ×) revealed that the major increments were constructed of smaller increments which in turn were composed of microincrements (Figs. 3, 4).

Differential etching caused the problem that not all the increments could be viewed at the same time. This was overcome through the use of suc-

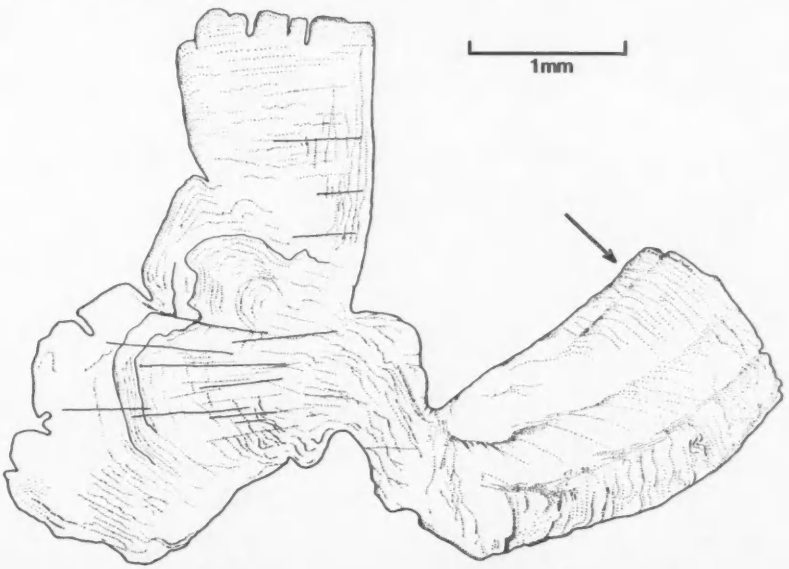

FIGURE 1.—Cross section of a bluefin tuna otolith showing the area (arrow) studied for microincrements. This area is on the rostral lobe of the otolith.

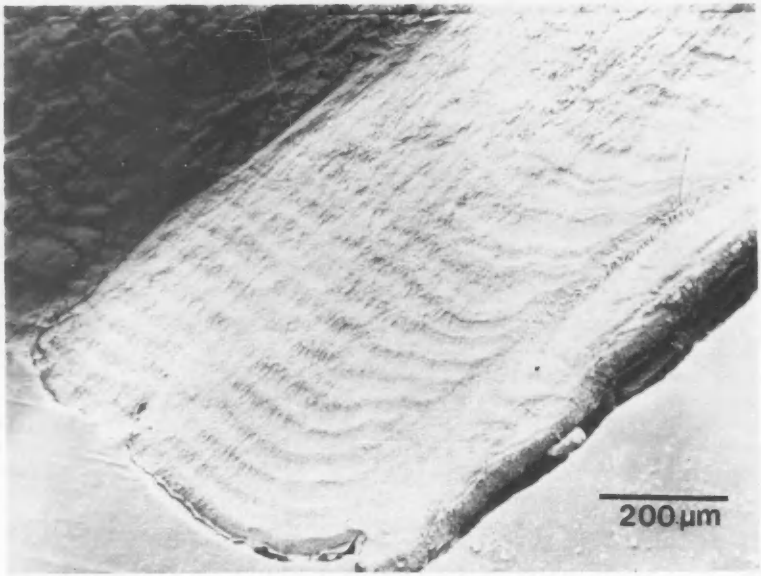

FIGURE 2.—Bluefin tuna otolith etched with EDTA which shows distinctive major increments. A short etching time gave good resolution to the outermost increments.

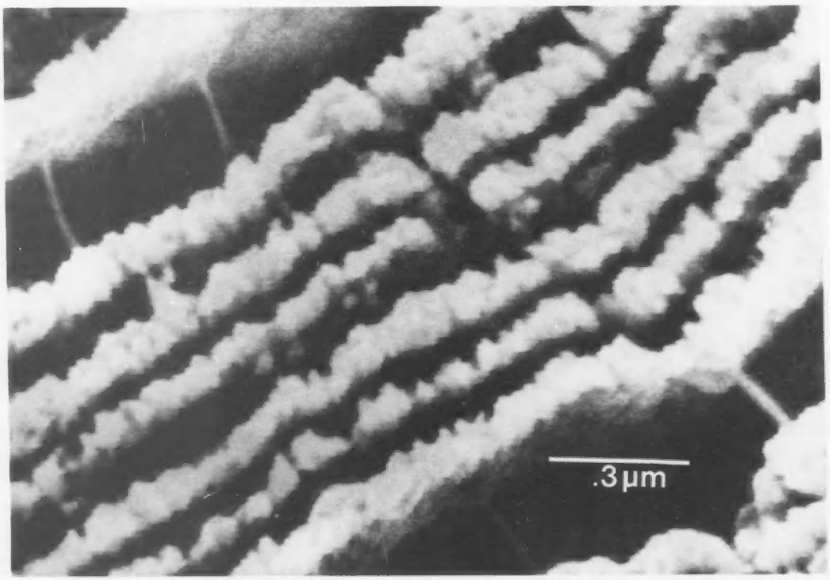

FIGURE 3.—Protein ridges of microincrements from a bluefin tuna. Strands of protein can be seen to interconnect the ridges.

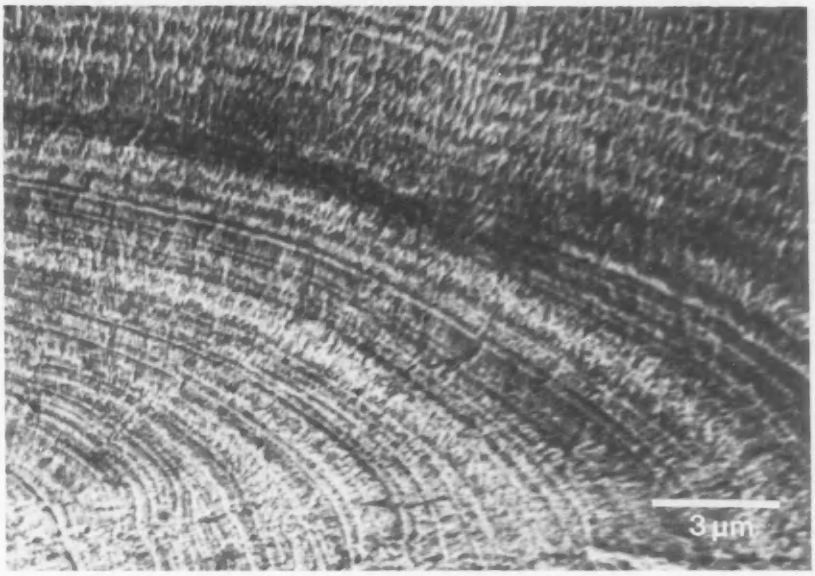

FIGURE 4.—Microincrements detected on the slope of a major protein ridge from a bluefin tuna. Differences in widths cause the yearly increments.

cessive cross sections which were etched for different time periods. This sequential etching made it possible to follow microincrements within the major increments. A difference in etching can be seen in Figures 2 and 5. Although major increments were clear in most etching times, the microincrements were not. Through the utilization of these techniques it was possible to obtain microincremental numbers for major increments (Table 1).

The microincrement counts in each major increment varied from 273 to 385 with the lowest count being found on the edge of the otolith. The summations of the microincrement counts for each fish were remarkably close and not significantly different ($P > 0.05$). Also, means of microincrements for each fish were not significantly different ($P > 0.05$) from the expected of 365 per year. These data increase the credibility of the microincrements being daily and present a plausible verification of the major increments as being annual.

Each microincrement is composed of a protein matrix with calcium carbonate crystals, in the aragonite crystal configuration, deposited within the matrix. Etching with EDTA dissolves the aragonite crystals leaving areas with a higher protein content to form discernible increments (Figs. 3, 4). Extended etching (times varied depending on the area of the otolith) can cause the protein ridges to collapse and prevent counting of the microincrements. Thus, etching times were critical to the acquisition of viewable increments.

TABLE 1.—Numbers of microincrements found in the major increments on the outer edge of the rostral lobe of the sagittae of four bluefin tuna, *Thunnus thynnus*.

Fish	1	2	3	4
Weight (kg)	496	381	405	470
Fork length (cm)	275	216	251	268
Sex	M	F	F	F
Estimated age[1]	25	19	19	24
Major increment	Counts	Counts	Counts	Counts
1	278	273	300	289
2	368	375	337	321
3	355	310	366	374
4	339	370	339	342
5	385	344	376	323
6	366	376	370	372
7	313	355	347	349
8	369	356	358	373
9	341	369	315	348
10	328	348	365	329
Total	3,442	3,476	3,473	3,420
Mean ± SD	344±32	348±33	347±25	342±27

[1]From counts of major increments by light microscopy.

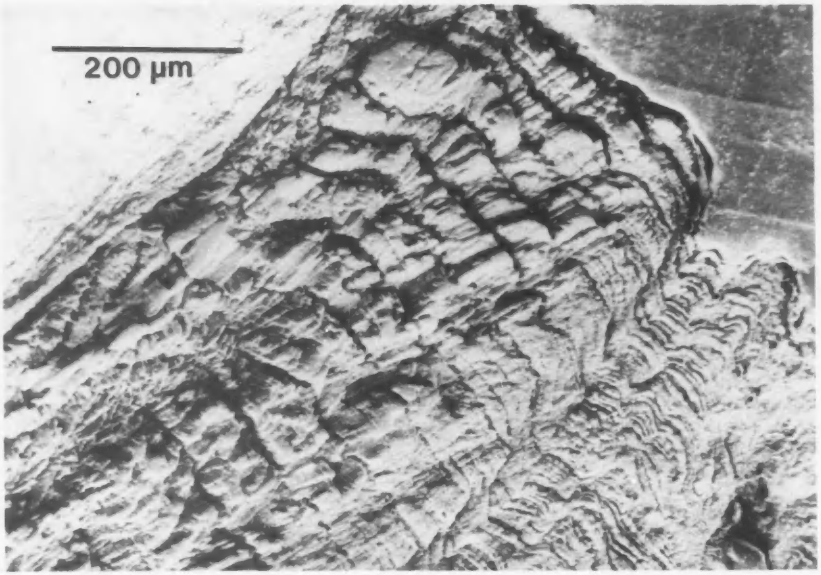

FIGURE 5.—Neighboring area of a bluefin tuna otolith shown in Figure 2 which demonstrates the uneven effects of etching.

The width of each microincrement varied in accordance with its position within a major increment. Microincrement width was probably a function of the time of the year when deposited. The widest microincrements were displayed between the ridges. Furthermore, the microincrements formed at the edge of the sagittae were wide and deposited during a time when the fish were fed large amounts of mackerel as part of the sea ranching operations. Observations on microincrement width suggest that wide microincrements were deposited during summer feeding and growth, while finer microincrements were deposited during the winter. It was these differences in width that accounted for the formation of yearly increments.

Most fish species investigated for daily age estimates have been found to possess daily increments in their otoliths (Pannella 1971; Brothers et al. 1976; Struhsaker and Uchiyama 1976; Taubert and Coble 1977; Methot and Kramer 1979; Steffensen 1980; Wild and Foreman 1980; Townsend and Graham 1981; Uchiyama and Struhsaker 1981; Radtke and Dean 1982). Thus, it is conceivable that the microincrements displayed in bluefin tuna otoliths are also daily. In tunas, Wild and Foreman (1980) studied daily increments in yellowfin and skipjack tuna, and Uchiyama and Struhsaker (1981) also investigated daily increments in yellowfin and skipjack tuna. Yellowfin tuna are found to deposit daily increments in both studies, whereas Wild and Foreman (1980) suggested that skipjack tunas have 25% fewer increments than would be expected if the increments occurred daily, while Uchiyama and Struhsaker (1981) advocated that daily increments did occur in skipjack tuna. In light of the present data, Wild and Foreman (1980) may have not detected increments formed during winter or colder periods. For giant bluefin tuna it is suggested that the microincrements are formed daily. If bluefin tuna did not deposit microincrements on a daily schedule, it would be expected that fewer daily increments would be detected in each major increment. Since this is not the case, it corroborates the idea that daily increments are formed in bluefin tuna otoliths and groups of daily increments form annual increments.

Otoliths may be the most useful hard structure for aging fish. Vertebrae and other hard structures are much more susceptible to resorption during times of physiological stress, while otoliths are

capable of permanently storing important ecological information since they are not susceptible to resorption (Mugiya and Watabe 1977). Otoliths have been shown to be the more accurate method of age determination in several fish species (Six and Horton 1977; Kimura et al. 1979). Otoliths are probably the most accurate means of age resolution in bluefin tuna.

In conclusion, the observation that microincrements in the sagittae of giant bluefin tuna about 365 in number for each outer major increment verifies the annual nature of these structures and strongly suggests that the microincrements are daily. Although it is not feasible to view large numbers of tuna otoliths by SEM techniques, the application of such techniques can provide answers to important biological questions.

Acknowledgments

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YEARLY CHANGES IN ABUNDANCE OF HARBOR SEALS, *PHOCA VITULINA*, AT A WINTER HAUL-OUT SITE IN MASSACHUSETTS

Information on the abundance of the harbor seal, *Phoca vitulina concolor*, population in New England consists of outdated estimates in the literature (King 1964; Maxwell 1967; Hewer 1974; Bonner 1976). A more recent series of unpublished reports (Richardson[1]; Knapp and Winn[2]; Kraus[3]; Gilbert and Stein[4]) suggests a harbor seal population which is increasing in numbers from its present breeding range north of Massachusetts southward into southern New England. A primary research need identified by Prescott et al.[5] was confirmation of this suspected increase in the harbor seal population throughout New England. This study summarizes available data on annual fluctuations in seal numbers since 1972 at one site in southeastern Massachusetts.

The study was conducted at Stage Point, Manomet, Mass. (lat. 41°55′N, long. 70°32′W). Harbor seals occur seasonally at Stage Point from late October through May (Schneider and Payne 1983). A rapid decrease in numbers occurs at this site in May (Schneider and Payne 1983), prior to the pupping season which occurs mid-May to mid-June in Maine (Richardson footnote 1; Wilson[6]). A few seals are reported throughout the summer but most move northward out of the study area by June.

The study site consists of a shoreline with a sandy cliff to 25 m. Sand, rock, and cobble extend from the base of the cliff into the water. Seals haul out exclusively on the larger rocks in the immediate subtidal zone from about 1-2 h before to 1-2 h after low tide (Schneider and Payne 1983). A similar haul-out pattern has been described at other rock-ledge sites in New England (Richardson footnote 1; Wilson footnote 6). Because of the synchronized haul out observed at Stage Point, the number of seals seen on the rocks is considered representative of the number of seals in the immediate vicinity (Schneider and Payne 1983) and, therefore, a useful index for monitoring changes in the abundance of harbor seals at this location.

Methods

Counts at Stage Point were made by direct observation within 2 h of low tide from the cliffs above the haul-out site. Schneider and Payne (1983) found that during 1979-80 the average number of seals observed at Stage Point peaked in January; therefore, the average number of seals ($\pm$SE) seen per daily count in January of each year was used in analyses among years. We transformed the January averages into logarithmic values, and the coefficient of correlation (r) from the linear regression was used to describe the relationship between the average number of seals seen per daily count in January 1972 and 1983.

In addition, air temperature, wave intensity, and human disturbance influence the total number of seals seen per daily count at Stage Point

[1]Richardson, D. T. 1973. Distribution and abundance of harbor and gray seals in Acadia National Park. Final report to National Park Service and Maine Department of Sea and Shore Fisheries, State of Maine Contract No. MM4AC009, 59 p.

[2]Knapp, C. L., and H. E. Winn. 1978. Harbor seals, New Hampshire to Long Island. Unpubl. rep., University of Rhode Island, Graduate School of Oceanography, Kingston, RI 02881, 36 p.

[3]Kraus, S. 1980. The population of harbor seals (*Phoca vitulina*) in southern New England. Unpubl. rep. of harbor seal workshop, 5 March 1980, Boston, Mass. New England Aquarium, Boston, MA 02109, 9 p.

[4]Gilbert, J. R., and J. L. Stein. 1981. Harbor seal populations and marine mammal fisheries interactions. University of Maine, Department of Forestry and Wildlife Resources, Orono, Maine. Annual Report to NEFC/NMFS/NOAA, Contract No. NA-80-FA-C-00029, 55 p.

[5]Prescott, J. H., S. D. Kraus, and J. R. Gilbert. 1980. East Coast/Gulf Coast cetacean and pinniped workshop. Final Report for Marine Mammal Commission, contract 79/02. Available National Technical Information Service, Springfield, VA 22151 as PB80-160104, 142 p.

[6]Wilson, S. C. 1978. Social organization and behavior of harbor seals *Phoca vitulina concolor* in Maine. Final Report to Marine Mammal Commission, Contract No. GPO PB 280-3188. Available National Technical Information Service, Springfield, VA 22151 as PB 280 188, 103 p.

(Schneider and Payne 1983). Prior to the winter of 1979-80, a record of environmental conditions at the time of the count was not maintained. Since it is not known to what extent weather or human disturbance near the haul-out site had on zero or near-zero counts previous to 1979-80, all daily counts in January with less than five seals were considered unreliable and excluded from the analyses. There were no available data for January 1973 or January 1977.

Results and Discussion

The average number of seals observed per daily count in January (Table 1) ranged from 9.3 seals (1974) to 88.25 seals (1980) with considerable variability among years. However, the observed number of seals was not randomly distributed among years; the January averages increased significantly ($P < 0.05$, $r = 0.63$, df = 9) between 1972 and 1983 (Fig. 1).

The average annual rate of increase since 1972 at Stage Point (based on expected values from the semilogarithmic regression, Table 1) was 11.9%/yr. The expected average number of seals per daily count in January at Stage Point (Table 1) doubled between 1973 and 1980.

The observed increase in the average number of seals at Stage Point has followed the termination in 1962 of a Massachusetts bounty on harbor seals and passage in 1972 of the Marine Mammal Protection Act. Rapid expansion of seal populations after the passage of protective legislation has been observed in the past (Hewer 1974; Bonner 1975; Everitt and Beach 1982) and has likely facilitated the increase since 1972 of the number of seals seen at Stage Point.

TABLE 1.—January averages of seals observed per daily count, 1972-83, at Stage Point, Manomet, Mass. n.d. = no data.

Year	No. daily counts	$\bar{x}$ no. (±SE) seals/daily count	Expected $\bar{x}$ no. seals/daily count[1]
1972	2	12.5 (6.52)	12.86
1973	n.d.		14.39
1974	3	9.3 (1.85)	16.11
1975	15	18.8 (2.32)	18.02
1976	2	34.0 (4.00)	20.17
1977	n.d.		22.58
1978	9	20.0 (3.07)	25.28
1979	9	35.56(7.00)	28.29
1980	28	88.25(6.06)	31.66
1981	18	21.67(6.92)	35.43
1982	18	21.88(2.94)	39.66
1983	19	48.00(5.63)	44.39

[1]From the linear regression: $y = 11.4898\ e^{(0.11263)x}$, $r = 0.628$, $P < 0.05$ (Fig. 1).

An increase in seal populations (after protection) due to unrestricted dispersion of juvenile seals has also been noted elsewhere (Bonner and Witthames 1974; Reijnders 1983). Bonner and Witthames (1974) suggested that the population of common seals, *P. v. vitulina*, located at the Wash in England, acted as a reservoir from which other reduced populations were replenished. Existence of a seal population in the Dutch Wadden Sea depends on unrestricted dispersal of juvenile seals from adjacent rookeries (Reijnders 1983). Since no rookeries occur south of Maine, it is apparent that the population increase seen at Stage Point (and throughout southern New England) has occurred through the southward dispersion of seals from Maine rookeries, after protection was established in Massachusetts.

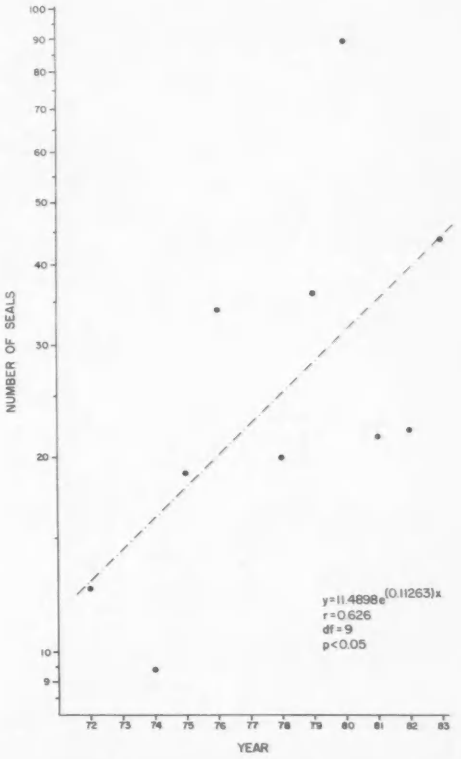

FIGURE 1.—Semilogarithmic plot of the average number of seals observed per daily count in January at Stage Point, Manomet, Mass., 1972-83.

Several investigators have reported an increase in seal numbers elsewhere in New England over the past decade. Gilbert and Stein (footnote 4) reported a total of 10,483 seals counted in June 1981 between Isles of Shoals on the Maine-New Hampshire border and the Canadian border. This nearly doubled the 1973 census of 5,786 seals reported for the same area by Richardson (footnote 1). Our data at Stage Point confirm this increase in southern New England.

The possibility does exist that the increase observed at Stage Point is merely the result of more thorough survey coverage in recent years; however, coastal bird observations were made regularly at Stage Point before 1973-74 by staff at the Manomet Bird Observatory. Any large number of seals would have been noticed during such counts.

The present harbor seal distribution, abundance, and breeding status in Massachusetts have changed considerably from the past. Allen (1869) reported "hundreds" of seals during the summer in Boston Harbor. As late as the 1930's and 1940's, harbor seals were permanent residents on Cape Cod (Prescott 1981) and pupping occurred throughout Massachusetts. Katona et al. (1983) suggested that the retention of the bounty until 1962 led to the extirpation of breeding activity in Massachusetts. The continued protection of an increasing harbor seal population throughout New England may result in expansion of the present breeding range southward into areas formerly used for pupping.

Acknowledgments

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POSTOVULATORY FOLLICLE HISTOLOGY OF THE PACIFIC SARDINE, *SARDINOPS SAGAX*, FROM PERU[1]

The use of the postovulatory follicle as a means of estimating incidence of spawning in multiple spawning fishes was originally developed by Hunter and Goldberg (1980) for the northern anchovy, *Engraulis mordax*, from southern California. This technique has proven to be quite useful for biomass assessment using the "Egg Production Method" (Parker 1980).

As a result of this work, the postovulatory follicle has assumed new importance. In the work of Hunter and Goldberg (1980), *E. mordax* were spawned artificially in the laboratory (Leong 1971). Fish were sacrificed at different time intervals, and histological conditions of the postovulatory follicles were noted. As an alternative to this method, in the current report we have aged postovulatory follicles of the Pacific sardine, *Sardinops sagax*, from Peru by establishing the time of spawning (egg collections) and by making periodic collections of *S. sagax*.

Methods

Samples of *Sardinops sagax* were collected during September-October 1982 near Chimbote, Peru (lat 09°05′, long. 78°35′). Ovaries were preserved immediately on collection in 10% neutral, buffered Formalin[2]. Later, samples from a total of 270 ovaries were dehydrated in ethyl alcohol and embedded in Paraplast. Histological sections were cut at 6μ. Slides were stained with Heidenhain's iron hematoxylin or Harris' hematoxylin followed by eosin counterstain.

Sardine egg samples from Peru indicated 0100 h to be the midpoint of the daily spawning interval (Smith[3]). Therefore, by knowing the hour of collection and assuming that spawning occurred around 0100 h, we calculated the approximate age of postovulatory follicles.

Results and Discussion

The sardine is a multiple spawning fish (Clark 1934), and during the spawning season we typically observe a mature yolk-filled mode of eggs representing the next spawning session and a vitellogenic mode for a subsequent spawning.

Postovulatory follicle, Day 0 (0-6 h after spawning)

The new *S. sagax* postovulatory follicles (Fig. 1A, B) were striking in their strong resemblance to the age 0-day postovulatory follicles of *E. mordax* (elapsed time from spawning <24 h) (Hunter and Goldberg 1980). The newly formed follicles of *S. sagax* contained many involutions or corrugations and were composed of columnar epithelium resting on a connective tissue theca. Nuclei had a basal location. The lumina occasionally contained eosinophilic granules of unknown origin (Hunter and Goldberg 1980) similar to those reported in the newly formed postovulatory follicles of *E. mordax*.

Postovulatory follicle, Day 1 (7-30 h after spawning)

These structures showed the beginning (Fig. 1C) of a breakdown in organization in comparison to day-0 postovulatory follicles. This included a size decrease to about one-half and marked degeneration of the columnar epithelial cell lining. Many epithelial cells had irregular shapes, vacuoles, and pycnotic nuclei. The convoluted structure was not as distinct as in day-0 postovulatory follicles. The linear arrangement of columnar epithelial cells was still evident. This is important, and constitutes the chief character that should be used for distinguishing day-1 from day-2 postovulatory follicles in *S. sagax*. This linear arrangement was absent in day-2 *S. sagax* postovulatory follicles.

Postovulatory follicle, Day 2 (31-53 h after spawning)

Degeneration of the *S. sagax* postovulatory follicle was clearly more advanced (Fig. 1D) at this stage. Distinguishing them from old atretic follicles is now a critical problem. Lumina were typically occluded and contained irregularly shaped cells with pycnotic nuclei, representing the final stages in the degeneration of the columnar epithelial cells that were previously so evident (Figs. 1A, B) in day-0 *S. sagax* postovulatory follicles. Vacuoles may be present. While the greatly convoluted structure that characterized earlier postovulatory follicles is no longer pronounced, there

[1]Publication No. 11 of PROCOPA.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]P.E. Smith, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. March 1983.

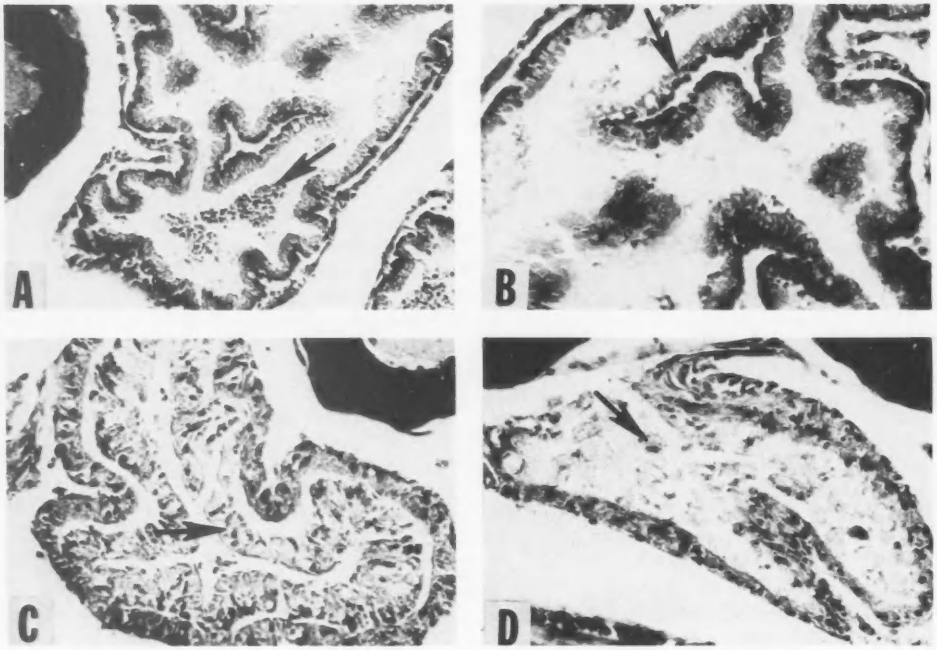

FIGURE 1.— Photomicrographs of *Sardinops sagax* postovulatory follicles. (A) Day 0, showing highly convoluted morphology. Note cluster of eosinophilic granules (arrow) in lumen (250×). (B) Day 0, showing columnar epithelial cell lining (arrow) (400×). (C) Day 1, columnar epithelial cell lining (arrow) undergoing degeneration. Underlying layer is connective tissue theca (400×). (D) Day 2, lumen contains scattered degenerated columnar epithelial cells (arrow) (400×).

should be some suggestion of it. We therefore recommend careful observation of the convoluted structure of day-0 and day-1 structures before attempting to identify day-2 structures.

A useful criterion for distinguishing day-2 *S. sagax* postovulatory follicles from advanced atretic follicles would be the presence of yellow granules (irrespective of staining) that are found in advanced atretic structures (delta atresia) (Lambert 1970). These were occasionally noted in *S. sagax*. The presence of these yellow granules which appear in nucleated clusters conclusively indicates atretic structures.

We did not use the artificial spawning technique (Leong 1971) for aging postovulatory follicles in *S. sagax*. However, we feel that estimating their age from periodic collections of fish, after the spawning time is established from collections of egg samples (as done herein), will prove to be a useful alternative method. This is particularly true in situations where facilities are lacking for laboratory-induced spawning. Laboratory-induced spawning studies using *S. sagax* will be useful to provide estimates of the accuracy of our classification scheme.

While there are numerous accounts of the occurrence of postovulatory follicles in marine fishes, there are few reports describing their longevity and subsequent degeneration. They have been described previously as being short-lived structures by Yamamoto and Yoshioka (1964) and Hunter and Goldberg (1980). More studies are needed of a wide variety of fishes before our knowledge of their histology and function is completed. Of utmost value will be investigations on how to distinguish conclusively between old postovulatory follicles and old atretic follicles.

Acknowledgments

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A NOTE ON SPAWNING OF THE PACIFIC MARKET SQUID, *LOLIGO OPALESCENS* (BERRY, 1911), IN THE BARKLEY SOUND REGION, VANCOUVER ISLAND, CANADA

In California, *Loligo opalescens* (Berry, 1911), has large spawning schools and spawn masses (McGowan 1954; Fields 1965; Hobson 1965; Cousteau and Diole 1973; Hochberg and Fields 1980). Spawns and spawning effort of this squid in the Pacific Northwest are poorly known and, to our knowledge, large spawns or spawning events have not been quantitatively described.

Loligo opalescens spawns regularly in Barkley Sound near Bamfield, British Columbia, (lat. 48°50.0′N, long. 125°07.5′W) in spring. We examined and measured portions of a spawn using scuba during early June 1982. The largest single capsule mass aggregation in our 200 × 50 m survey area was measured. Adjacent areas of smaller solitary egg capsule masses were surveyed using transects to determine overall spawn dimensions and percent cover of individual capsule masses. Dimensions of 23 typical masses were determined. Four representative masses were collected; the number of capsules in each was counted; and from each, 10 capsules were randomly selected and the number of eggs in each capsule was determined. These eggs were examined microscopically to determine the developmental stage, which was compared with the embryological stages illustrated in Fields (1965) to estimate the time of deposition.

The spawn, including areas of continuous and solitary egg capsule masses, was larger than the area surveyed, as the spawn extended below our deepest possible survey depth. Within our survey area, the largest capsule mass aggregation covered about 69.3 m^2 and averaged 0.28 ± 0.09 m (n = 4) in thickness. The mean density of the individual masses was 1.3 ± 0.1/m^2, and the mean area covered by 23 masses was 0.28 ± 0.14 m^2/mass, with a range of 0.13-0.66 m^2. The mean number of egg capsules per solitary mass was 1,937 ± 912 (n = 4), with 149 ± 35 eggs/capsule (n = 40). Thus, the total number of eggs per isolated mass was 288,000 ± 125,000. For the large areas of isolated masses, the potential number of larvae produced per 100 m^2 ranged from 19 to 58 × 10^6, with a mean of 37 × 10^6. The number of potential larvae from the single large aggregation of 69.3 m^2 ranged from 27 to 204 × 10^6, with a mean of 72 × 10^6.

Based on embryological stages observed, deposition probably occurred during the night of 31 May-1 June 1982. Small squid schools were observed spawning near the survey area on that date. None of the embryos were old enough to be deposited before 31 May, and all were of the same embryological stage.

Female squids from Californian populations deposited about 21 capsules, each containing about 200 eggs, in one night (Fields 1965); fecundity data from our region are not available. Hochberg and Fields (1980) stated that *L. opalescens* females produce 180-300 eggs/capsule. Our data indicate a lower mean value of about 150 eggs/capsule. If each female deposited 20 capsules, the large measured aggregation would be the result of about 24,000 females.

In conclusion, northern *Loligo opalescens* populations form large spawning schools and deposit massive egg capsule masses similar to those observed in the Californian populations.

Acknowledgments

We thank the directors of the Bamfield Marine Station and the Friday Harbor Laboratories for the use of the respective facilities. Two anonymous reviewers provided helpful suggestions.

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ARITHMETIC VERSUS EXPONENTIAL CALCULATION OF MEAN BIOMASS

Mean biomass ($\overline{B}$) within a time interval (t) is used in the Ricker method of estimating yield per recruit and can be calculated either arithmetically as

$$\text{(i)} \qquad B_t = \frac{B_t + B_{t+1}}{2}$$

or exponentially as

$$\text{(ii)} \qquad B_t = \frac{B_t\,(e^{G_t - Z_t} - 1)}{G_t - Z_t}$$

(Ricker 1975). The choice of calculation method may influence the yield estimates and consequently the determination of optimal levels of exploitation.

Ricker (1975) and Paulik and Bayliff (1967) alluded to the importance of the difference in magnitude between instantaneous growth and total mortality rates ($G_t - Z_t$). They indicated that if the difference was small, arithmetic and exponential calculations approached one another. Ricker suggested using small intervals if the rates are rapidly changing. In this paper we 1) examine the difference in the two estimates of mean biomass as a function of the instantaneous rates of growth and mortality, and 2) reexamine the consequences of the choice of mean biomass estimates on estimates of equilibrium yield per recruit using data previously employed by Ricker (1975) and Paulik and Bayliff (1967), showing that under many conditions, exponential estimates of mean biomass are preferable.

The difference between arithmetic and exponential estimates of mean biomass increases rapidly as $G_t - Z_t$ increases in a positive direction, but diverges less rapidly when $G_t - Z_t$ increases in a negative direction. When B_t is arbitrarily taken in unity, the relationship is satisfactorily represented by a polynomial regression (Fig. 1).

With many fisheries it is only possible to estimate instantaneous fishing mortality (F_t) on an annual basis. Thus, a large interval must be used. The larger the interval, the more likely it is that $G_t - Z_t$ is of a magnitude that would cause significant differences in estimates of $\overline{B}_t$ calculated arithmetically and exponentially. Also, in heavily exploited fisheries there may be a large difference between growth and mortality rates within an interval especially at older ages.

We employed Ricker's (1975:242-243, table 10.3) example of bluegills from Muskellunge Lake to illustrate the difference between the two methods of computing mean biomass. This set was chosen because Ricker's data have been used previously as a historical data set and are readily available through his text. Mean biomass was computed arithmetically in the text example and also by Paulik and Bayliff (1967), who used the same data to introduce their computer program. We used the data in two separate runs to compute yield per

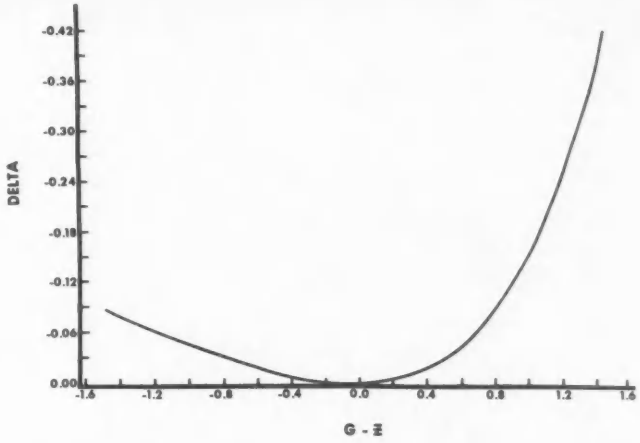

FIGURE 1.—Difference between arithmetic and exponential calculations of mean biomass when $dt = 1.0$ and $B_t = 1.0$, DELTA $= B_t(B_t, \exp - B_{t,\text{arith}}) = B_t^a \{0.0061 + 0.0037\,(G_t - Z_t) - 0.1095\,((G_t - Z_t)^2) - 0.0491\,((G_t - Z_t)^3)\}$, $r = 0.998$.

recruit. In one, B_t was computed arithmetically, and in the other it was computed exponentially (Fig. 2). In both runs, the number of survivors was followed across the intervals and biomass was tracked within each interval. There were obvious significant differences. Evaluating various F-multiples and ages of entry, when B_t was calculated arithmetically, the maximum yield exceeded the maximum biomass of the stock (5,522.6

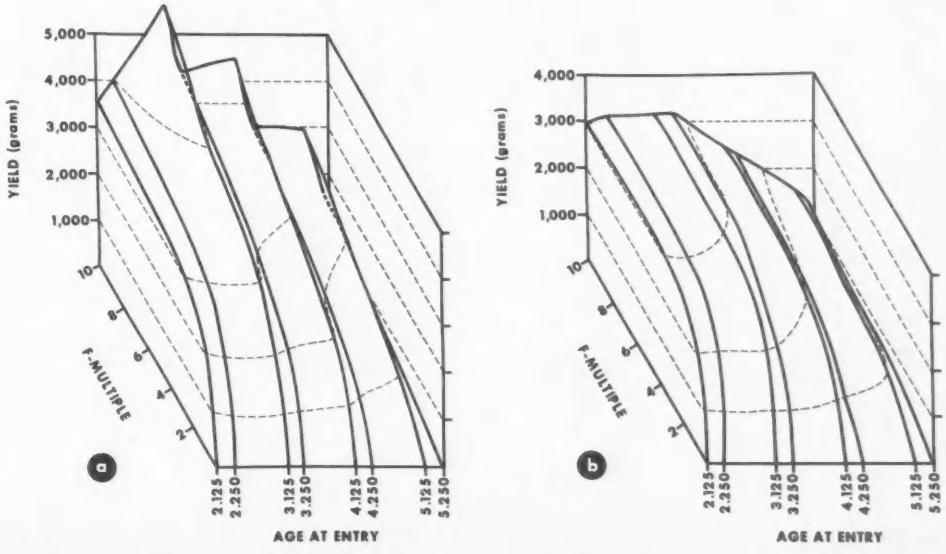

FIGURE 2.—Yield per recruit estimates for bluegills of Muskellunge Lake calculating mean biomass a) arithmetically and b) exponentially (data from Ricker 1975: table 10.3).

g vs. 3,439.2 g) when F-multipliers were large, which is impossible. Maximum biomass of the stock was estimated at F equals zero; the time intervals used were four one-eighth of a year intervals followed by one-half year intervals. Despite the small intervals, the difference between the yield per recruit estimates was large, indicating a need to minimize the $G_t - Z_t$ difference if B_t is calculated arithmetically, regardless of the size of the time intervals. Therefore, in similar circumstances and for the example data set, we recommend that B_t be calculated exponentially.

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